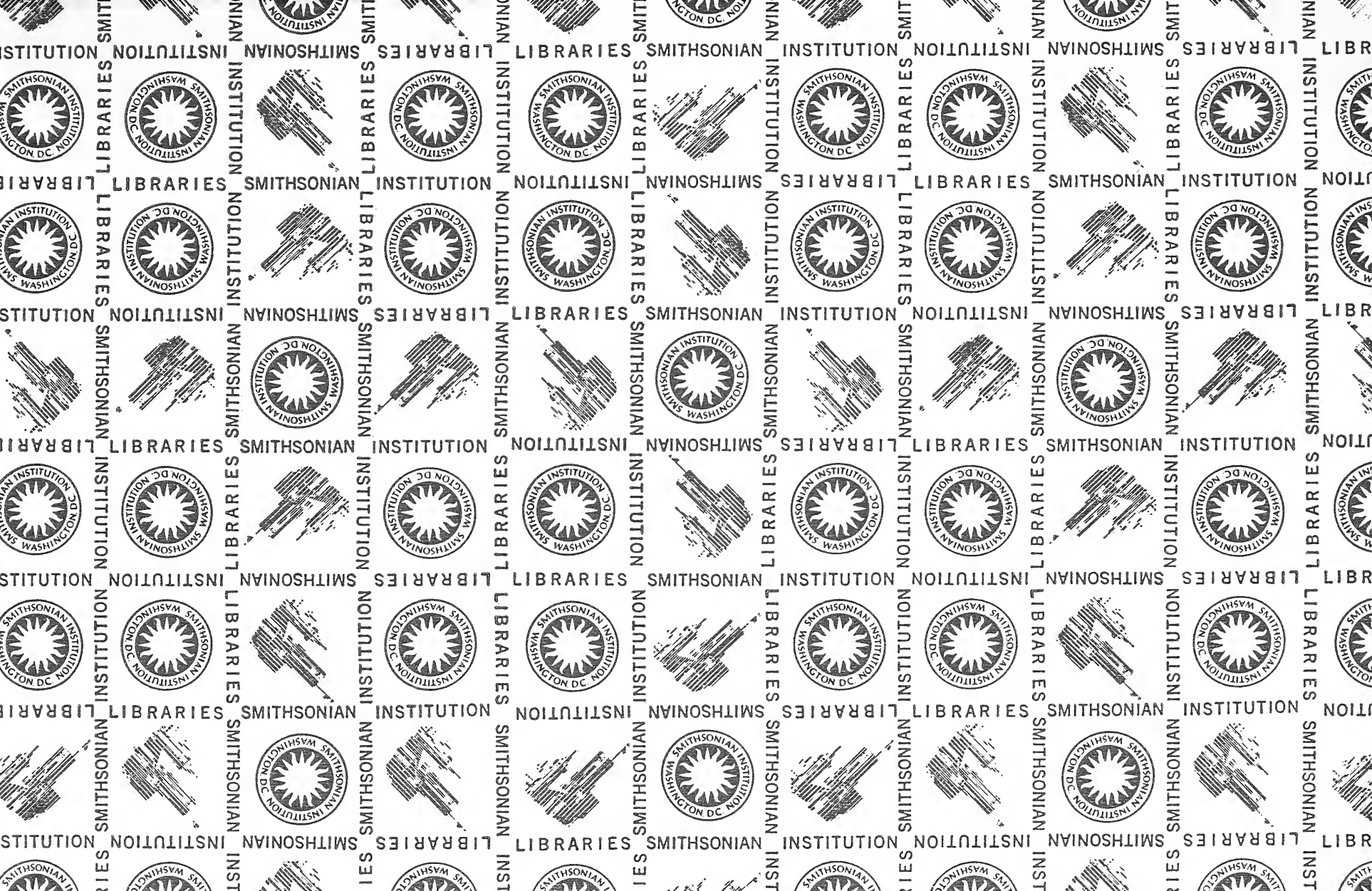
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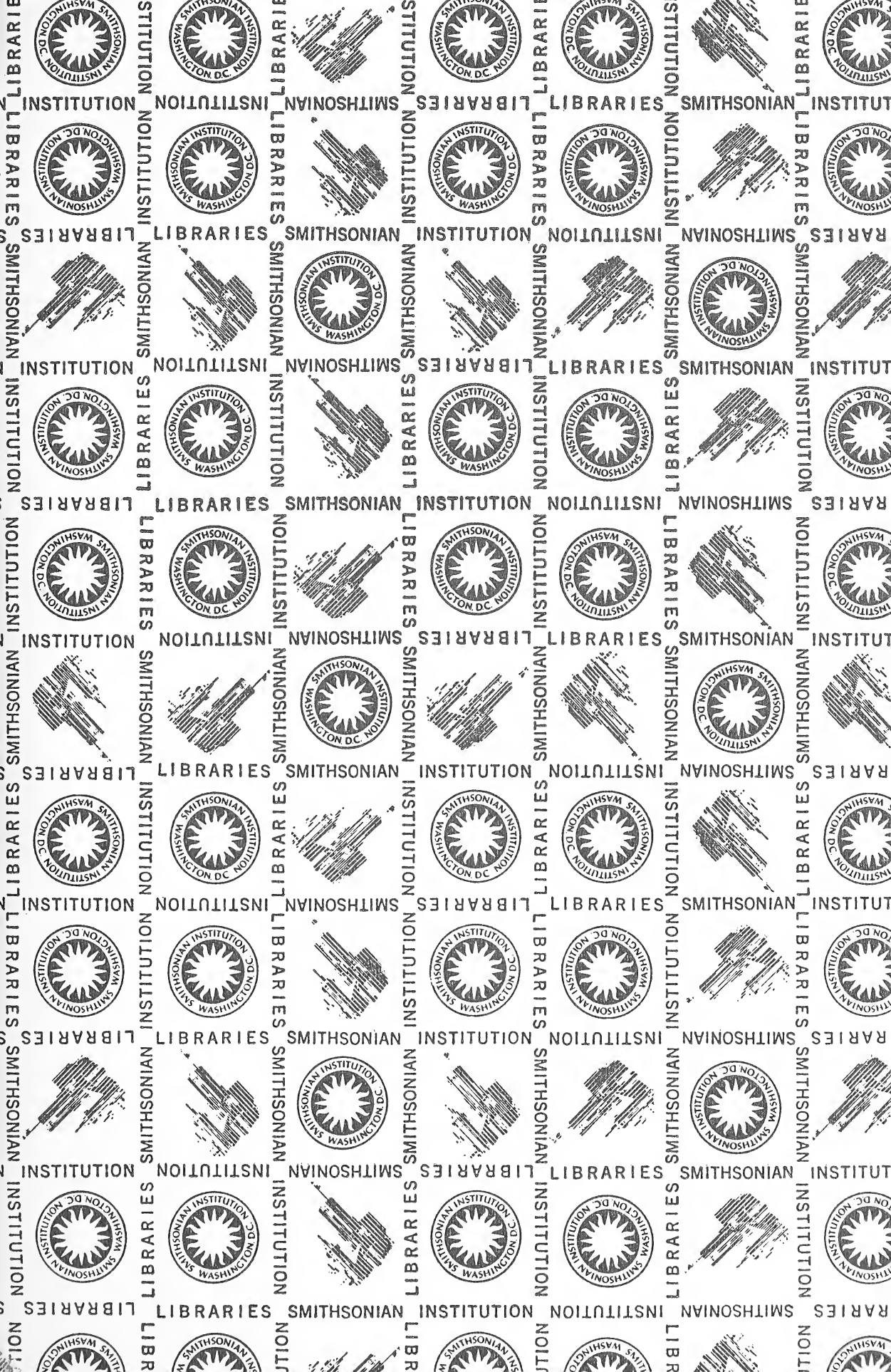
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Cover illustration: A male *Tetragnatha extensa* from Carlisle, Massachusetts. Original color photo by Joe Warfel of Arlington, Mass. Photograph made with a handheld Olympus OM-1 35mm camera, macro lens, telescoping extension tube and manual flash.

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VISUAL BRIGHTNESS DISCRIMINATION OF THE JUMPING SPIDER *MENEMERUS BIVITTATUS* (ARANEAE, SALTICIDAE)

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ABSTRACT. It was observed that the jumping spider *Menemerus bivittatus* lives on light surfaces as well as on dark surfaces, hunting prey which is lighter or darker than the surface the spider is on. From these observations arises the question about the brightness or contrast discrimination abilities of this spider. The orientation response was recorded for 14 spiders to a moving circular prey-stimulus varying from white, through grey, to black, against a white, grey or black background. When the stimulus was darker than the background, there was a rapid increase in response as the stimulus gets darker. This rapid change in response with stimulus brightness did not occur when the stimulus was lighter than the background. These results reveal a high contrast discrimination ability and also a dependence of the response on the overall stimulation conditions.

The visual system of jumping spiders (Salticidae) is highly developed when compared to other families of spiders. Like most spiders, jumping spiders have four pairs of eyes. The most specialized are the anterior median eyes (AM), that are used in prey pursuit (Land 1971). It has been suggested by Land that the AM are capable of color vision. The other eyes function primarily to detect prey movement and to elicit orientation toward prey (bringing the prey into the visual field of the AM eyes).

The jumping spider *Menemerus bivittatus* (Dufour) is common in Southern Brazil and can be found throughout the year in almost all homes of São Paulo. Retreats are generally located in the highest part of doors or window frames or under an outside overhang.

Preliminary observations of the habitat preferences of *M. bivittatus* revealed that (1) spiders hunted on either a dark surface (e.g., black painted poles) or a light surface (e.g., wall of buildings) and (2) on both of these surfaces both light colored prey (e.g., small Diptera) and darkly colored prey (e.g., *Musca*) were taken. There appeared to be no difference in prey catching efficiency between the different backgrounds. Since *M. bivittatus* has a light appearance (greyish brown with black stripes) the spider is very conspicuous on a black ground and almost invisible on light colored walls.

These observations raised the question of whether jumping spiders are capable of discriminating differences in contrast between stimulus and background. Since single visual receptor cells are known to react with graded potentials to light intensity, the physiological capability for contrast discrimination appears available. The most likely mechanism is a neural circuit that enhances brightness differences and contrast in the same way as is known for many vertebrates and invertebrates. However, the question remains on how contrast discrimination is integrated into specific behaviors, such as prey catching and mate recognition. The reflexive behavior of jumping spiders to orient themselves and the AM eyes toward the prey after its detection by the secondary eyes (Land 1972) is a very simple behavioral response that can be easily observed and recorded in the laboratory.

The purpose of this experiment was to establish the psychophysical brightness discrimination function measured by this orientation response for different levels of ground brightness. Another question was to find if the function for the discrimination of a light stimulus against a dark background is symmetrical to a dark stimulus against a light background. Lack of symmetry between the functions would indicate an increased ability at prey detection in one of the situations and might suggest that the spider would have a preference for one of the hunting conditions.

METHODS

Subjects.—Ten adult female and four adult male jumping spiders, *Menemerus bivittatus*, were collected on the campus of São Paulo University and taken to the laboratory where they were held individually in petri dishes in 12/12 h light/dark illumination. Individuals ranged from 6–12 mm

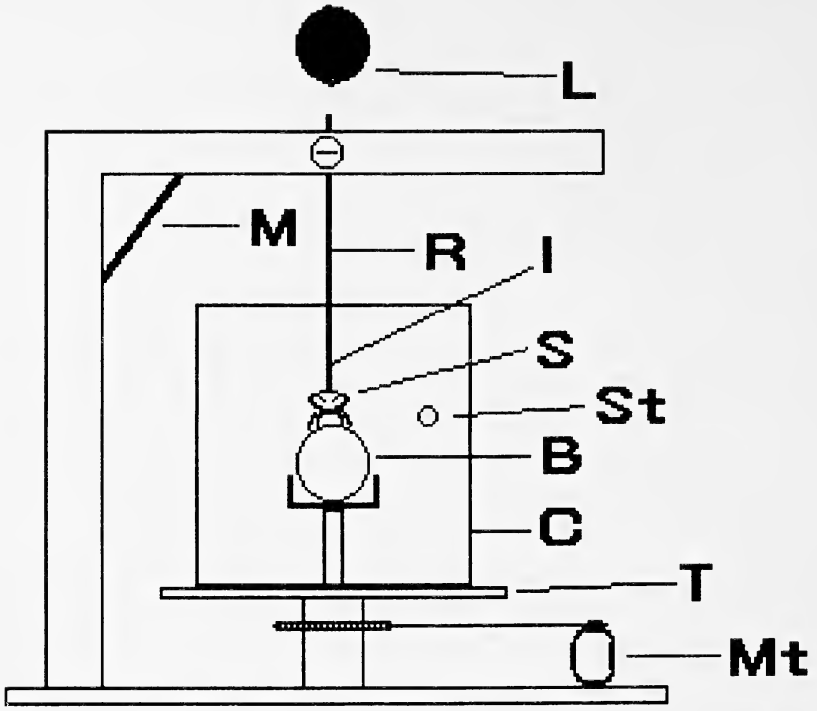

Figure 1.—Apparatus used in the experiment. The spider (S) after being anesthetized was glued to the head of the insect needle (I) that was inserted into the rod (R) that was adjusted so that the spider touched lightly the styrofoam ball (B). Around the spider the painted cylinder (C) with the stimulus (St) that could be easily interchanged, was positioned on the revolving turntable (T) driven by the motor (Mt). Observation was made through the mirror (M). The lamp (L) provided constant and uniform light of 155 lux measured at 90° on the surface of the styrofoam ball.

in total length. Live *Musca* were offered to each spider once a week. The spiders survived for several months under these conditions making it possible, if necessary, to divide the whole experimental procedure into several experimental sessions on different days.

Experimental procedure.—Prior to an experimental session the spider was lightly anesthetized with carbon dioxide so that the head of an insect needle could be glued with wax to the rear part of the prosoma. Care was taken to avoid covering the eyes with wax. After the spider completely recovered from anesthesia, the animal was placed into the experimental apparatus (Fig. 1). The experimental apparatus was basically a motor driven turntable on which three different cylinders, constituting the background for the visual stimuli presented to the spider, could be made to turn in either direction. On the axis of the cylinder a styrofoam ball (25 mm in diameter) lay loosely in a Teflon cup. The spider, held by the needle glued to its prosoma and an adjustable rod, could walk on the styrofoam ball in any direction, turning or rolling the styrofoam ball. The slightest turning or walking movement of the spider (and consequently of the styrofoam ball) could be observed through a mirror attached over the apparatus. Observation through a mirror was preferred to direct observation in order to reduce disturbances of the spider. Overall illumination was provided by a daylight ring light (Toshiba, Japan) producing an illumination of 155 lux at the top of the styrofoam ball at 90°.

White, grey and black glass cylinders (250 mm diameter, 300 mm height) were used for the background against which the spider could see the stimulus. The white cylinder had a reflection density of d = 0.11, the grey 0.56, and the black of 2.08. Density was measured with a reflection densitometer (X-Rite Inc., Grandville, Michigan, USA, Model B318) calibrated for d = 0.00 with a standard calibration card (TiO_2 coated). The glass cylinders were painted from outside (so that the inner glare was the same) except for an 8 mm diameter "hole" left transparent, coplanar to the spider, where the stimuli could be

Table 1.—Mean and SD of the response probability for the white, grey and black backgrounds for each presented stimulus. $n = 14$ for all cases.

Stimulus density	Background					
	White		Grey		Black	
	mean	SD	mean	SD	mean	SD
0.11	0.01	0.00	0.09	0.06	0.52	0.09
0.27	0.13	0.05	0.15	0.12		
0.31	0.29	0.09	0.15	0.12	0.59	0.08
0.36	0.39	0.15	0.14	0.09		
0.50	0.78	0.09	0.00	0.00	0.53	0.10
0.56	0.80	0.14	0.00	0.00		
0.58	0.86	0.12	0.00	0.00	0.46	0.11
0.76	0.90	0.09	0.85	0.05		
0.86	0.94	0.06	0.93	0.03	0.38	0.07
0.91	0.98	0.02	0.96	0.02		
1.01			0.99	0.01	0.33	0.08
1.15					0.25	0.07
1.52					0.18	0.07
2.08					0.08	0.03

applied from outside without producing any shadow or border. The stimulus thus subtended an angle of about 4° at the spider's eyes. With the white background, stimuli of the following reflection densities were used: 0.11, 0.27, 0.31, 0.36, 0.50, 0.56, 0.58, 0.76, 0.86 and 0.91. With the grey background the same stimuli were used, and also a darker one of 1.01 reflection density. For the black background, stimuli of the following reflection densities were used: 0.11, 0.31, 0.50, 0.58, 0.86, 1.01, 1.15, 1.52 and 2.08. The stimuli were produced by painting white paper with the same paint used for the glass cylinders, mixing from the white and black paint in different quantities.

Each animal was tested for the white, grey and black backgrounds but in different orders. For each background the stimuli were presented in random order. Five trials were run on each stimulus/background combination. Each trial consisted of five complete turns of the cylinder (alternating left and right turns). Each turn was started with the stimulus exactly behind the spider's back, out of its visual field (this could be verified by the fact that the spider never responded to a moving stimulus at that position) and took around 20 seconds to be completed, resulting in a mean angular velocity of the stimulus of 18 deg/s. For every turn of the cylinder it was manually recorded if the spider made a response toward the stimulus or not. For each density value of the stimulus the overall response probability was calculated by dividing the number of cylinder turns that elicited a response by the total cylinder turns. With few exceptions, there was no doubt that a movement of the spider was directed to the moving dark or light spot. When, for some reason the spider entered spontaneous walking activity, the experiment was interrupted until the spider assumed its typical alert posture.

After finishing the stimuli presentations for one background density, the same procedure was repeated for a different cylinder. The spiders stayed responsive for up to 3 or 4 hours.

RESULTS AND DISCUSSION

The mean and the standard deviation (SD) for the response probabilities for each background and stimulus are given in Table 1. The SDs calculated among animals are fairly small, suggesting that the recorded orientation response is rather reflexive. The response probability curves for the white, grey and black backgrounds are given in Fig. 2.

The response curve for the white background varies from almost zero for a white stimulus (zero contrast with the background) to almost 100% for a 0.91 stimulus density (maximum contrast). This experimental condition would conform to a situation were the spider hunts for dark prey on a light background, which seems to be the situation to which the spider is best adapted, since the spider itself has a light color and most of the prey like *Musca* are dark in color.

The response curve for the black background has a quite different shape, not being just the mirror image of the first curve as might have been expected. Response probability declines very slowly with increasing stimulus darkness. The highest response probability is somewhat lower than 60% for a light grey stimulus (reflection density of 0.27). For a lighter stimulus (0.11) that produces a higher contrast with the black background, the response rate is even lower. The difference is statistically significant (Student, $df = 13$, $t = 2.57$, $P < 0.05$). Of the 14 spiders tested, 12 presented a lower response rate for the brighter stimulus. This suggests that the spider is not responding just to the contrast value between stimulus and background. The spider might be responding in part to the appearance of the stimulus disregarding the background, or some other unknown factors are influencing its behavior.

The response curve for the grey background shows, as expected, the lowest response proba-

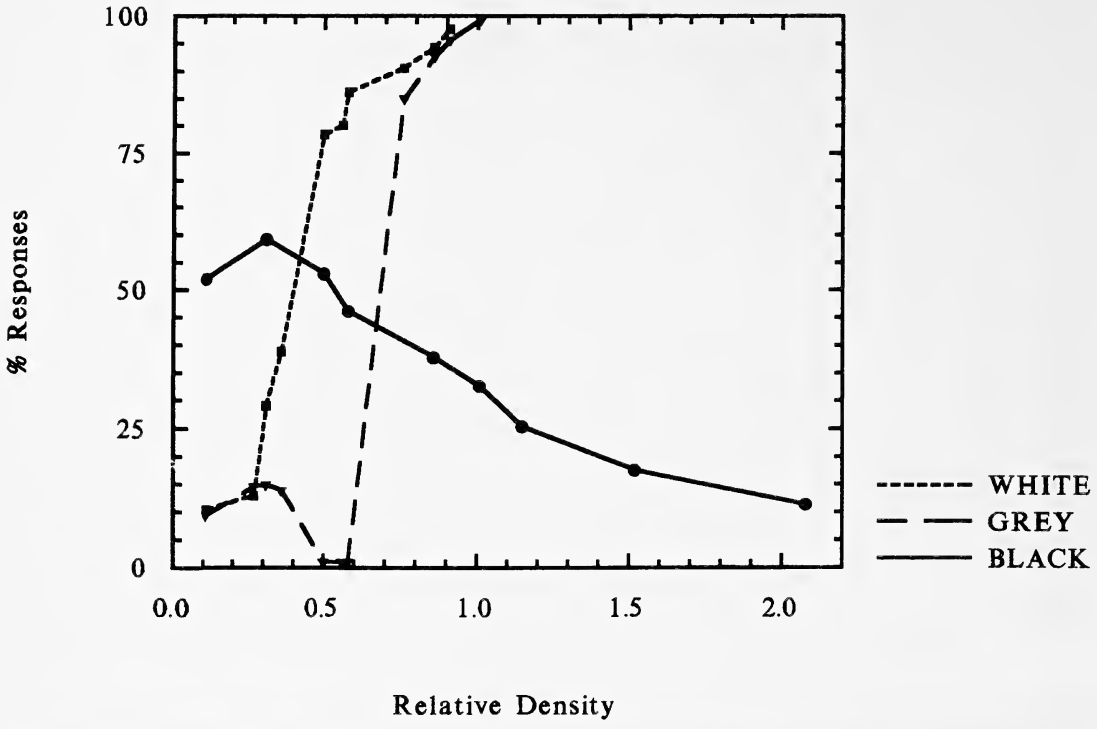

Figure 2.—Response probability curves for the white, grey and black backgrounds (cylinders) to stimuli of different greyness, from white to black.

bility for the stimulus density that equals the background density (relative density of 0.50, 0.56 and 0.58) where the contrast is close to zero. The part of the curve where the stimuli are darker than the background has more or less the same shape and steepness as the curve for the white background. With reversed contrast, the highest response probability is again not for the highest contrast condition, but for stimuli in the relative density range of 0.27–0.36. Out of the 14 records, for nine the response rate for the lightest stimulus (0.11) was lower than for the next darker one, two were equal and three reversed. The Student test for the difference of the means for both stimuli revealed a near to significant probability ($df = 13$, $t = 1.98$, $P > 0.05$). These results favor the idea that the response is not only guided by the contrast between prey and background, but also by the absolute lightness of the prey.

The lower response maximum of 60% for the stimuli against the black background could suggest that the spiders are visually less alert or aroused in this situation since the overall light level within the black cylinder must be lower, due to less reflection of the constant illumination provided by the lamp on the top of the cylinder. If this were the case, visual alertness would also be lowered with the grey cylinder. Since in the grey cylinder a response rate of 100% was achieved for darker stimuli, visual alertness differences, if any, caused by different illumination levels, do not explain the results.

These overall results could be compared to the description of Land (1972) who, in an experiment where jumping spiders responded to black or white stripes, found that the pursuit response to black stripes was given to the leading edge, while the response to white stripes to the trailing edge. Land concluded that the stimulus must always move in such a way as to cause sequential darkening of adjacent photoreceptors. The results of the present experiment could be explained in the same way, since the spider could be responding to an edge of the stimulus, although the stimulus was small. For the light stimulus on the dark background, the spider would be responding to the trailing edge of the stimulus or, what would be exactly the same, to the leading edge of the dark background. This would mean, that the stimulus is now the "huge" background which of course had lost its "prey characteristics" to the spider, explaining the lower response rate

for this condition. An alternative interpretation would be that the spider in this experiment is reacting to the small stimulus as a whole, as long as it has enough contrast with the background, but with a clear preference for dark stimuli on lighter backgrounds. Drees (1952) showed that the courtship behavior of *Epiblemum scenicum* (Salticidae) reveals well-developed visual acuity. Such acuity might also be important in prey capture. However, Blest (1985) found that the prey capture sequence could be elicited by stimulus shapes quite different from normal prey, as in the study reported here. Therefore, it seems that the orientation response which initiates both prey capture and courtship is mainly guided by the contrast of the stimulus against the background.

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CIRCADIAN RHYTHMICITY AND OTHER PATTERNS OF SPONTANEOUS MOTOR ACTIVITY IN *FRONTINELLA PYRAMITELA* (LINYPHIIDAE) AND *ARGYRODES TRIGONUM* (THERIDIIDAE)

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ABSTRACT. Endogenous biological rhythms are apparently found in all eukaryotic organisms. The most ubiquitous of these, the circadian rhythm, functions to synchronize physiology and behavior with diel changes in the environment. Data presented here demonstrate that, in the linyphiid spider *Frontinella pyramitela* (Walckenaer) and in the theridiid spider *Argyrodes trigonum* (Hentz), a circadian rhythm modulates locomotor activity in some individuals but not in others. The data also show (a) that higher-frequency endogenous rhythms play a part in determining the patterns of motor activity, and (b) that intervals between bouts of activity are influenced by aperiodic processes that appear to be stochastic.

Much of the behavior of animals in the field is closely correlated with environmental stimuli: the detection of predators or prey stimulates flight or pursuit, the presence of a rival results in agonism, the arrival of a mate elicits courtship or bonding rituals, and changes in the thermal environment lead to altered postures or positions. The internal state of an animal (e.g., the time since its last meal, the size of its gonads, or the presents of parasites and pathogens) also influences behavior, sometimes profoundly.

Among the most ubiquitous of internal state variables is the endogenous circadian clock, which has been particularly well studied since the pioneering work of Aschoff (1954) and Bünning (1963). Although the cellular and molecular bases of biological clocks remain obscure, their utility is well documented: they facilitate prediction of periodic environmental events, make celestial navigation possible, and enable the temporal organization of internal events. Because the overt manifestations of these clocks are often subtle, they are most easily and profitably studied in animals isolated from confounding environmental stimuli, including conspecifics and such *Zeitgebers* as light cycles. Under those conditions of isolation, an animal's behavior is said to be freerunning (i.e., showing the natural period of the circadian clock).

In spiders, endogenous rhythmicity has been suggested by data on diel rhythms under natural conditions (e.g., in *Amaurobius*, Cloudsley-Thompson 1957), and has been confirmed in a very few species under constant conditions (e.g., in *Cupiennius salei*, Seyfarth 1980; for other references, see Cloudsley-Thompson 1987). Moreover, in work with the linyphiid spider, *Frontinella pyramitela* (Walckenaer), my laboratory has found that internal programs quite distinct from circadian clocks appear to govern the timing of certain spontaneous (i.e., internally driven) behaviors related to courtship (Suter 1990) and cohabitation (Suter & Walberer 1989). The present study constitutes the beginning of an elucidation of the programs, both circadian and other, that underlie the onset and cessation of spontaneous behaviors in *F. pyramitela*.

METHODS

I captured adult females of both *F. pyramitela* and *A. trigonum* in Dutchess County, New York, during June, 1992, and immediately installed each in an open-ended glass cylinder. I placed the cylinder in an aluminum trough and inserted that into a plexiglass holder which could house eight such troughs. One end of each cylinder was partially occluded by an infrared sensitive phototransistor (Radio Shack SDP8403-301) and the other end was sealed by a circular microscope coverslip behind which was mounted an IR light-emitting diode (Radio Shack SEP8703). The assembled apparatus, with the simple electronic circuits used to drive it, is shown in Fig. 1. I enclosed the apparatus in a light-tight chamber (20 cm × 24 cm × 18 cm) in which the relative humidity was maintained at 100% and temper-

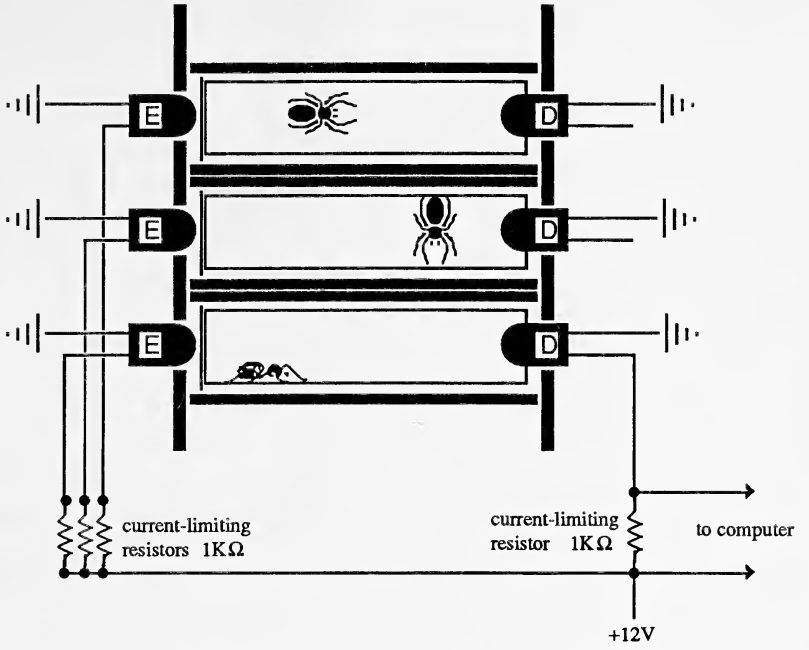
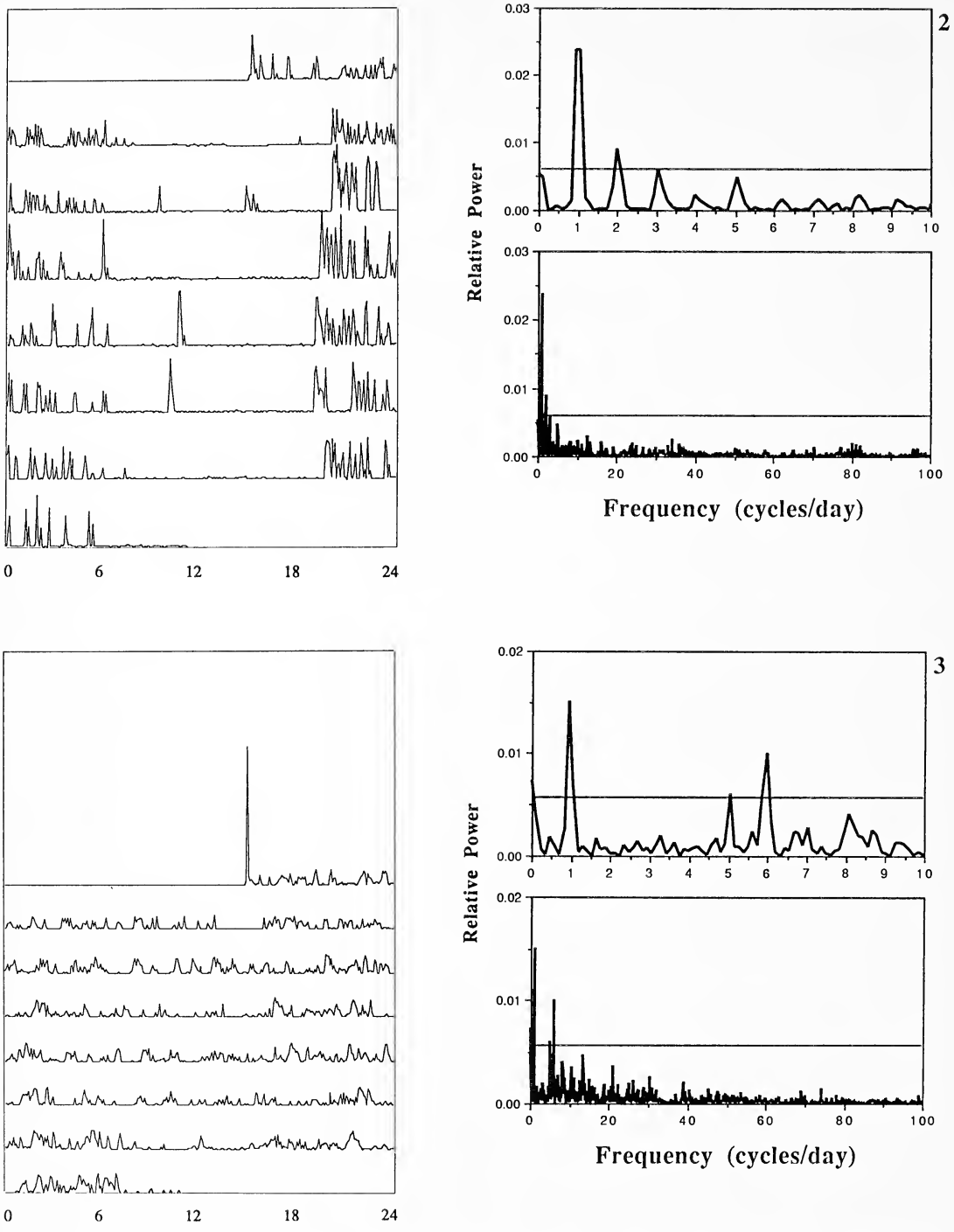


Figure 1.—Schematic diagram of the apparatus used to house spiders and detect their motion. IR emitters (E) and detectors (D), coupled to a computer, formed the motion-detection system. The spiders themselves were enclosed in glass cylinders 1 cm in diameter and 4.5 cm long.

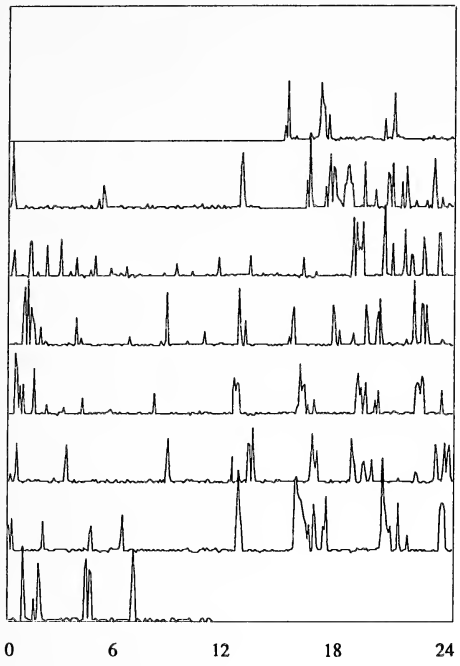
ature was constant at 24 ±1 °C. The electronic driving circuits, which generate some heat, were mounted outside the chamber. Output from each IR phototransistor was digitized and recorded by computer (hardware: Macintosh IIci with National Instruments NB-MIO-16 I/O board; software: a customized data-logging program written in LabVIEW 2). At each of the eight channels, amplitude was measured at 2 ms intervals (500 Hz) and the standard deviation of the amplitudes collected during 1.6 s was the datum recorded as an index of activity during that period. (Preliminary tests had shown that, because of the multiple paths the IR light could take in a chamber, grooming motions and other movements of appendages did not cause fluctuations in phototransistor output. Thus high-frequency fluctuations were unlikely. Moreover, power spectra of phototransistor outputs from chambers containing rapidly moving spiders recorded at 500 Hz with no averaging revealed that there was no significant energy at frequencies > 1.0 Hz).

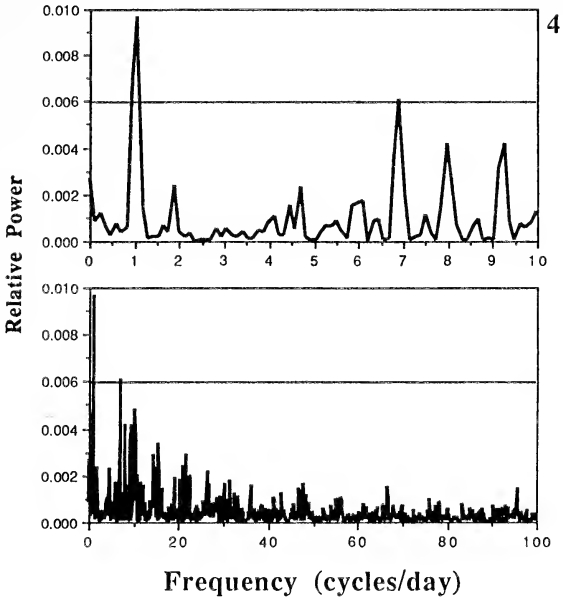
The activity of 14 *F. pyramitela* and 5 *A. trigonum* was recorded during the study. The maximum continuous length of time in the chambers was 11 days for a group of 7 *F. pyramitela*. While in the chambers, the spiders were neither fed nor watered. Because of the high relative humidity, desiccation was not a problem for the spiders, and fasting for periods longer than 11 days can be tolerated by *F. pyramitela* (Suter 1985) and by other species (Anderson 1974). Two separate experiments involving *F. pyramitela* were run: in one the spiders were maintained in constant darkness (DD) throughout their 8-day isolation, and in the other the chamber enclosing the spiders was lit for 8 hours each day for 11 days (LD, onset of light daily at 1100 h; illumination by orange, green, and red LEDs provided 7.7 lux at each chamber). The single experiment that involved *A. trigonum* was carried out in DD.

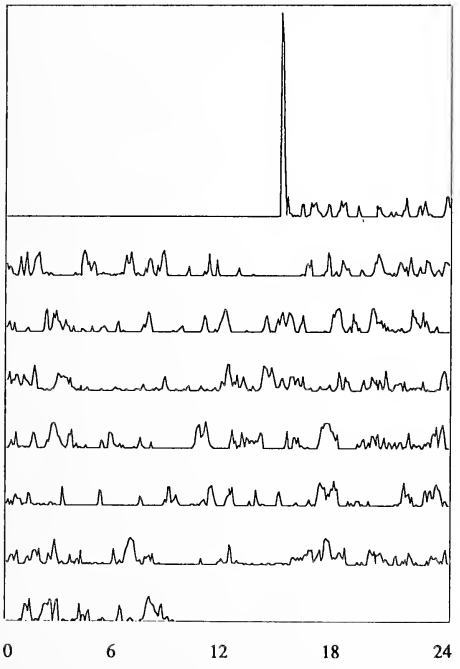
The digitized activity records of individual spiders were analyzed in two ways. (1) Spectral Analysis I: A Hamming window (to minimize the artifacts caused by truncation of a signal) was applied to the recorded string of activity/inactivity periods which was then analyzed by fast Fourier transform (FFT) and displayed as a power spectrum showing the proportion of explained variance in activity as a function of frequency. Significant peaks were identified by a chi-square method described elsewhere (Suter & Forrest, in press) which could reveal time-based periodicities such as a circadian rhythm. For the detection

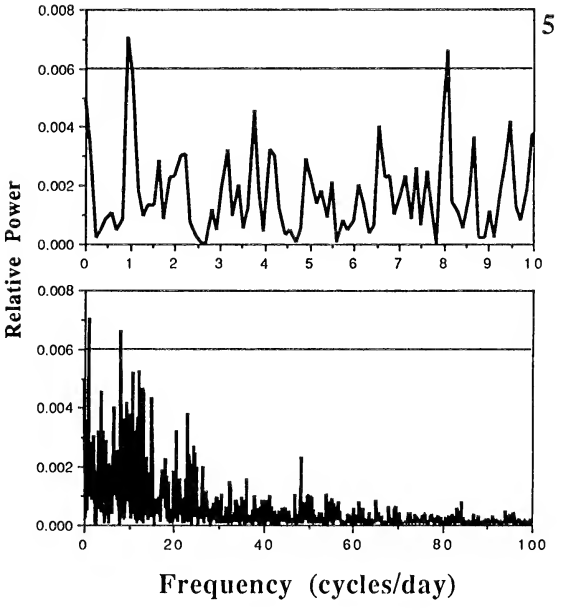


Figures 2–8.—Activity of *F. pyramitela* under conditions of constant darkness (DD). Graphs on the left show activity as a function of time, with days shown sequentially from top to bottom. FFT analysis of these data resulted in the power spectra shown on the right in each figure. The power spectra are shown at two scales to elucidate both the overall pattern (lower panel) and the peaks between 0 and 10 cycles/d (upper panel). In each of these power spectra (as in all others in this study), the first component (furthest to the left) should be ignored because it reflects the entire data set and not oscillations within the data set. Much of the explained variance is concentrated near 1.0 cycle/d, but significant peaks are also found at higher frequencies. Peaks at or above the horizontal lines are significant at $\alpha = 0.01$.









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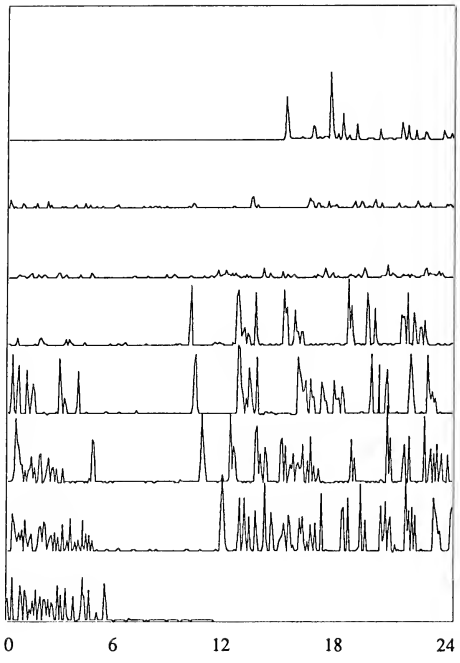

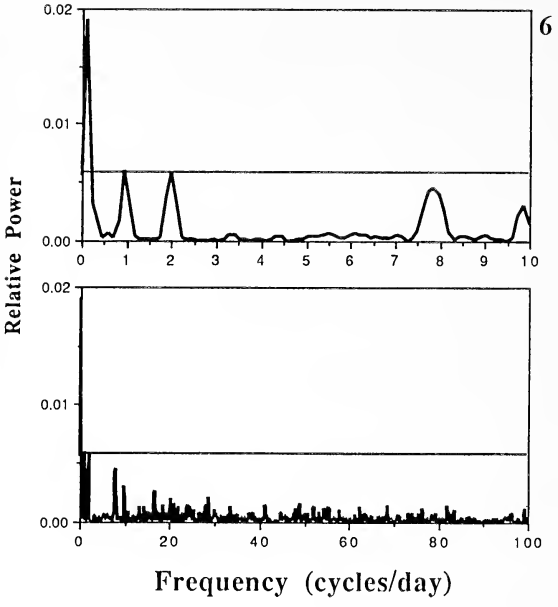

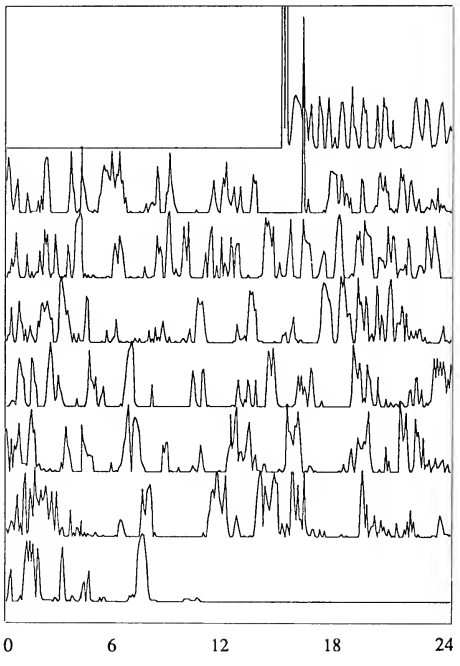

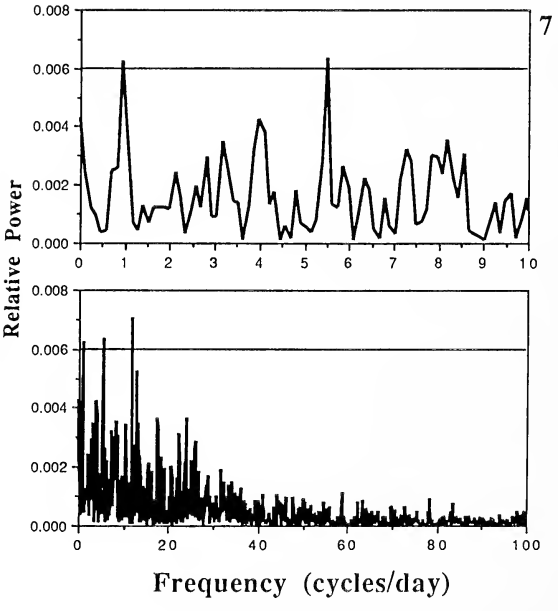

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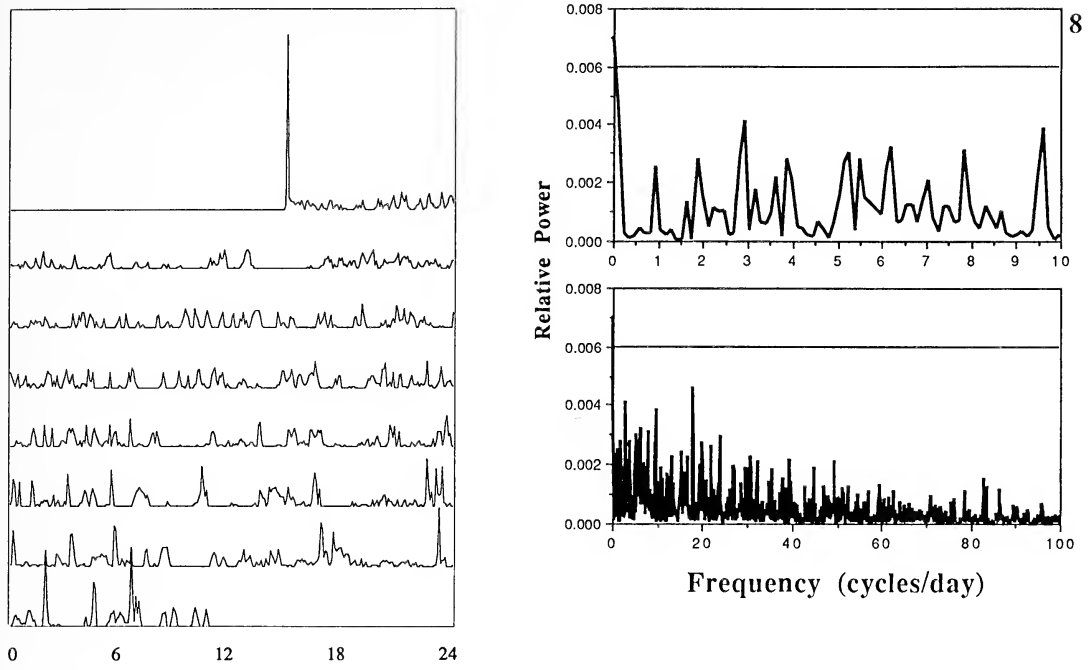

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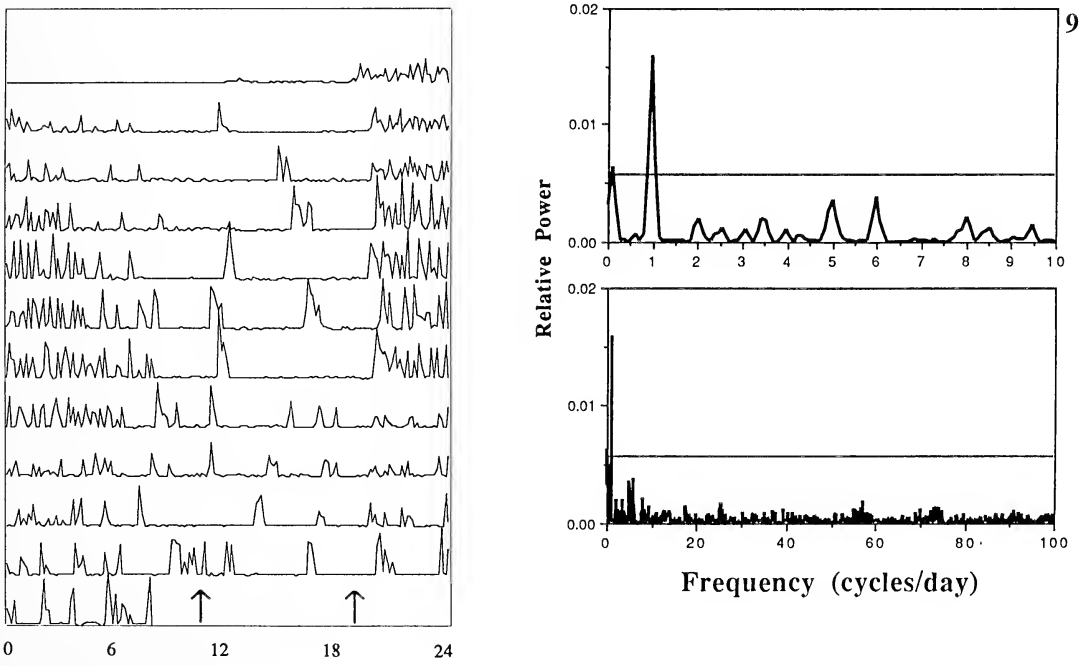
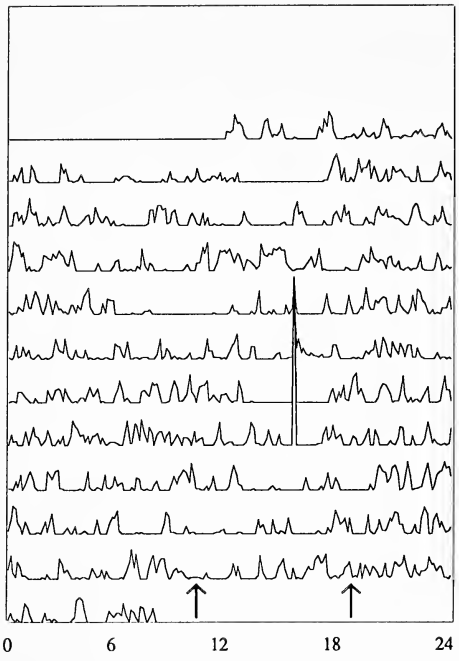
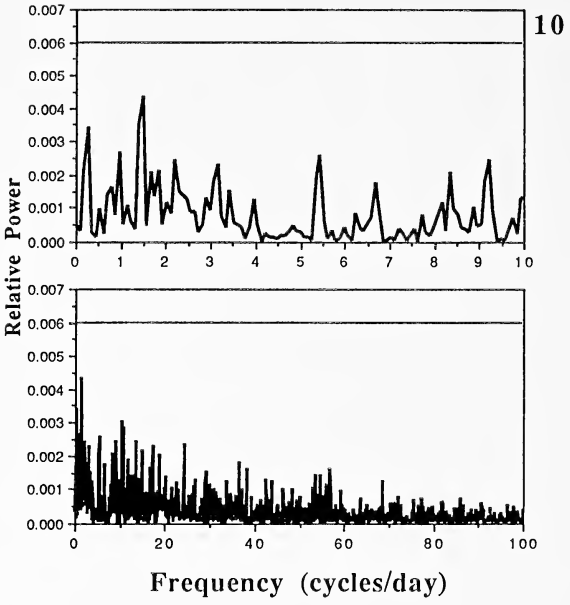
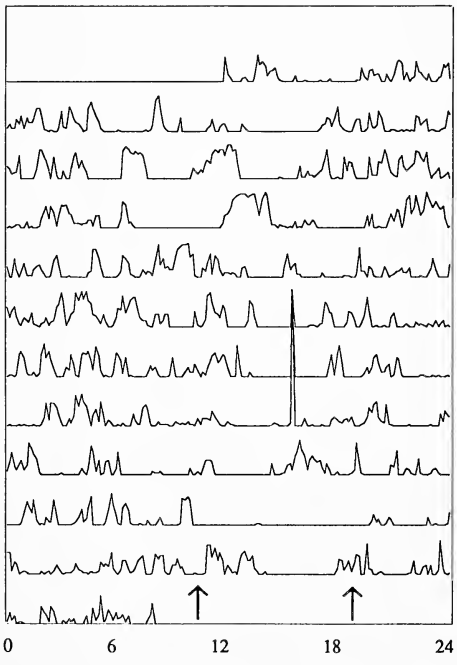
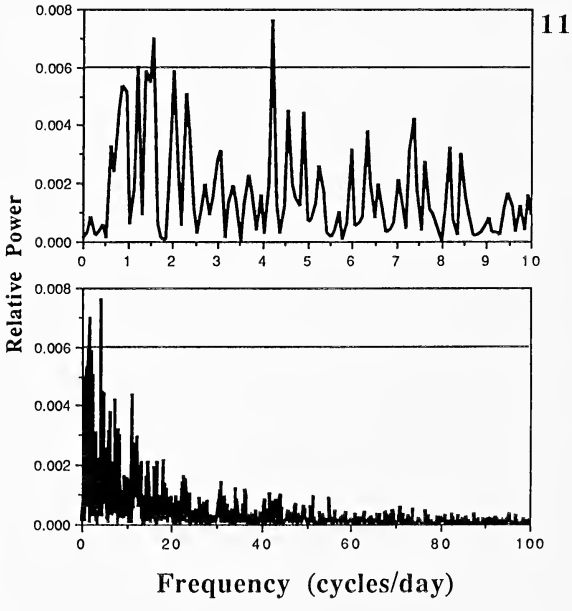


Figures 9–15.—Activity of *F. pyramitela* under conditions of a 24-h photoperiod (LD) in which lights were on between 1100 and 1900 h (arrows). See the legend for Figs. 2–8 for an explanation of the layout.

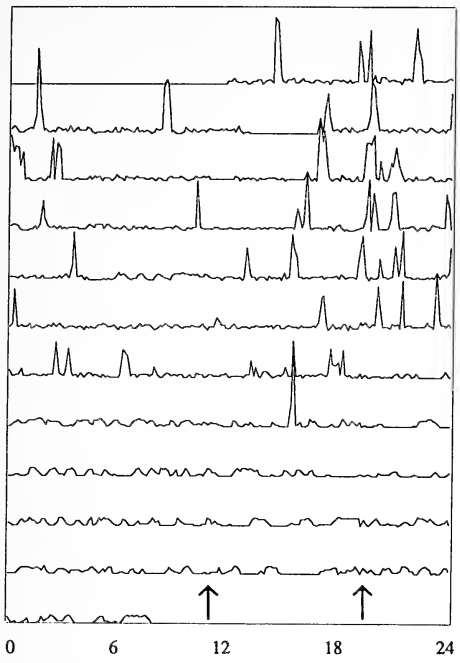


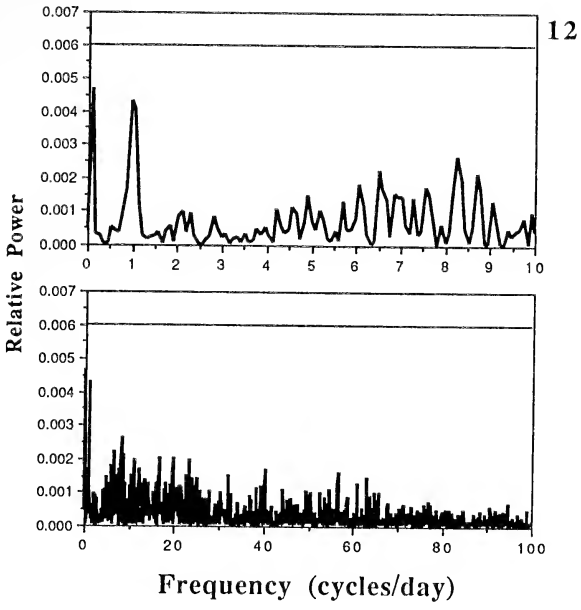


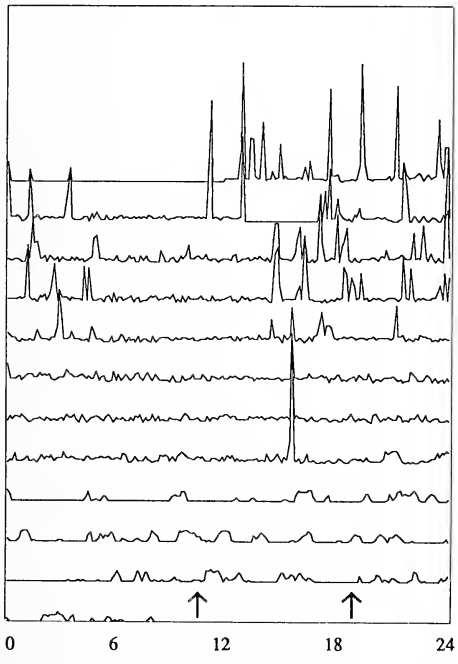


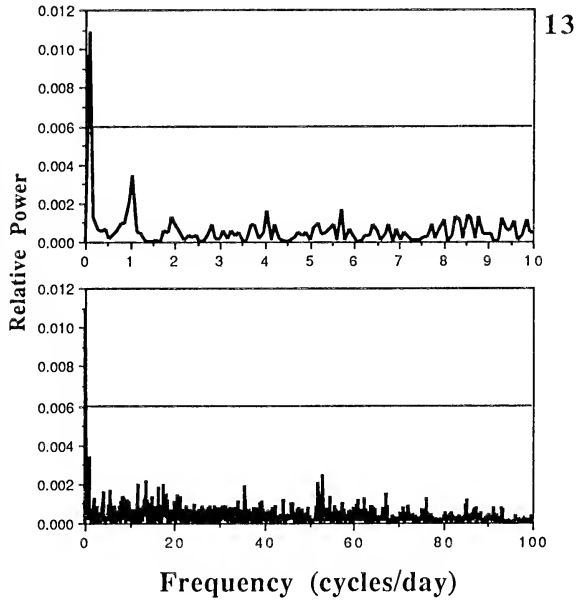


Figures 9–15.—Continued.









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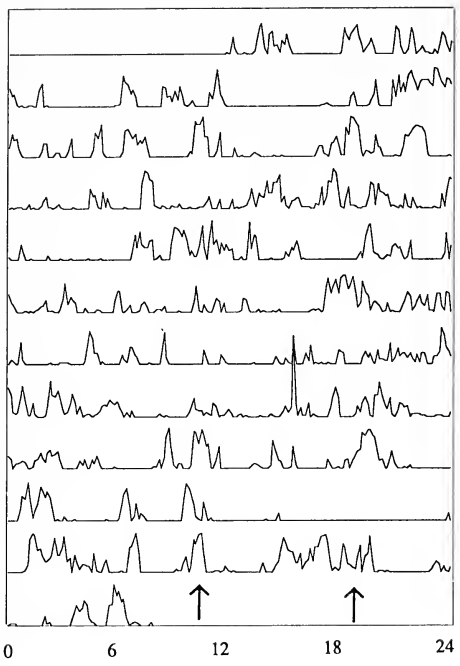

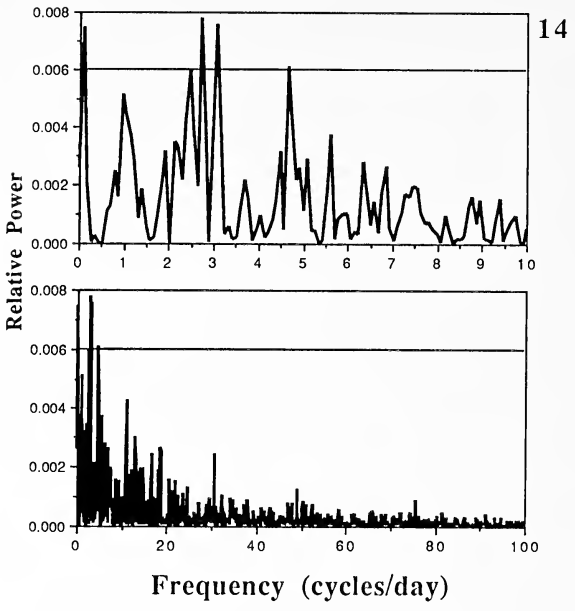

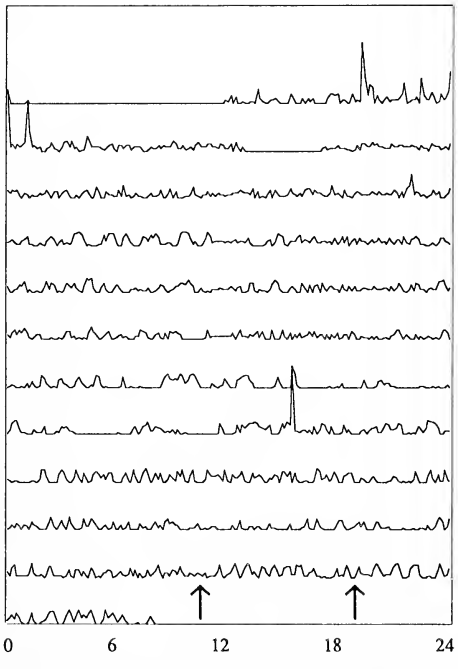

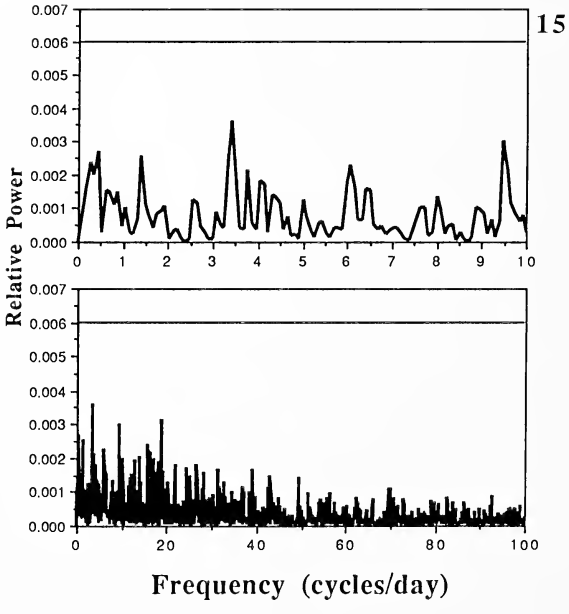

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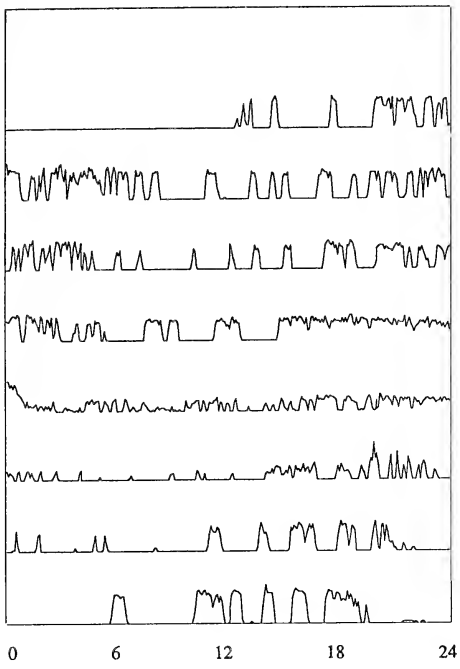
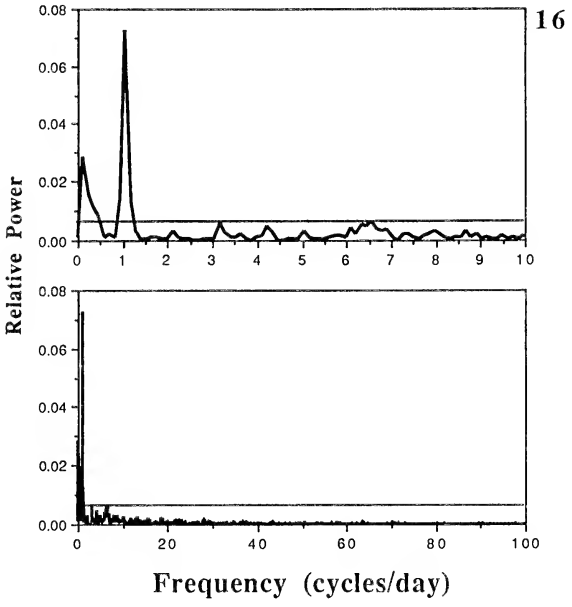
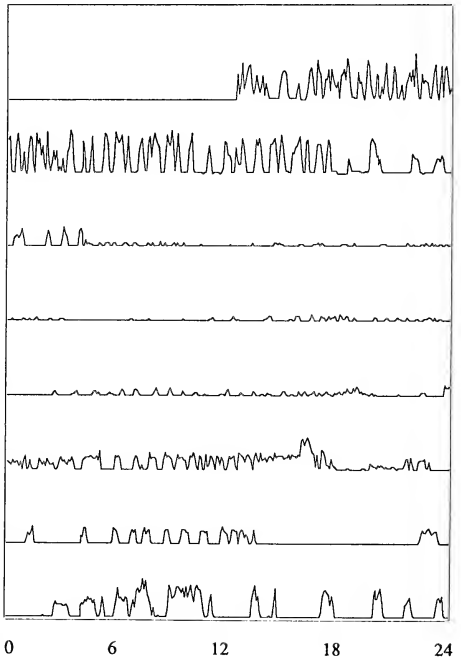
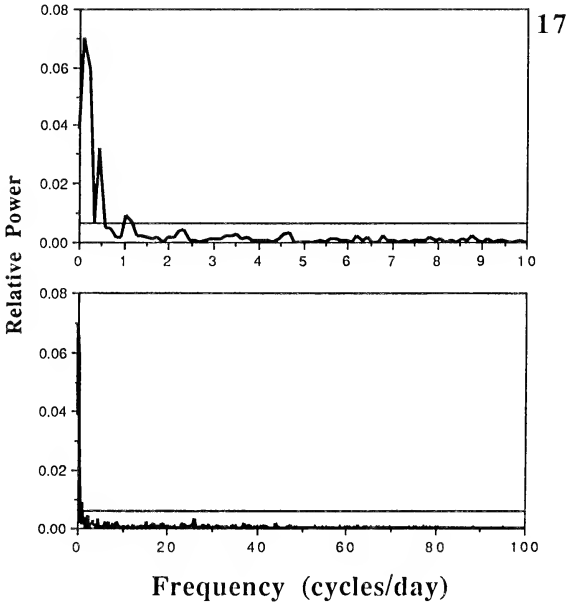
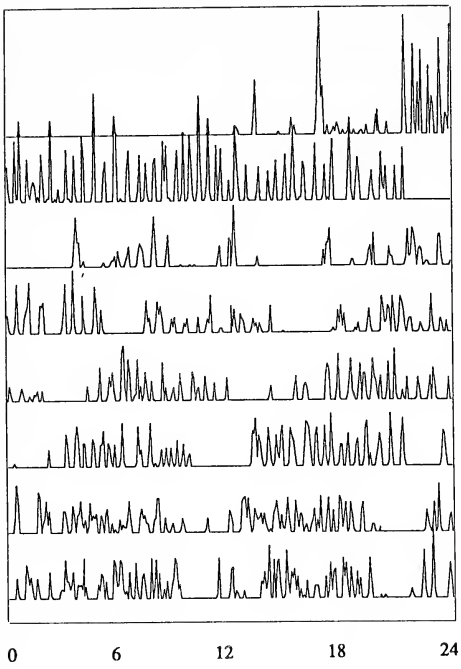


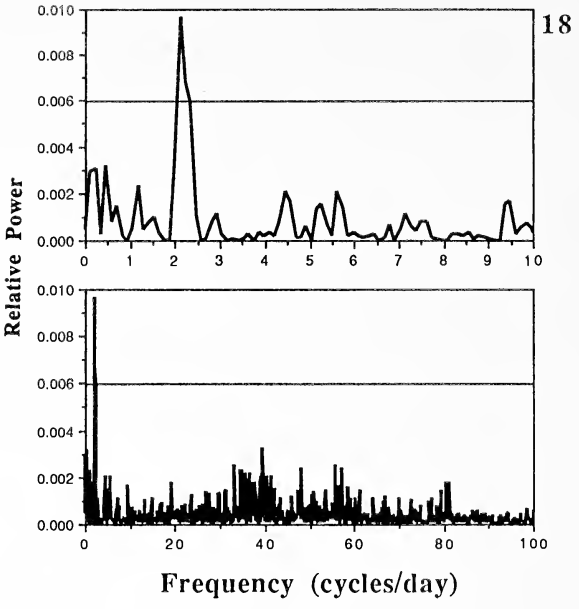


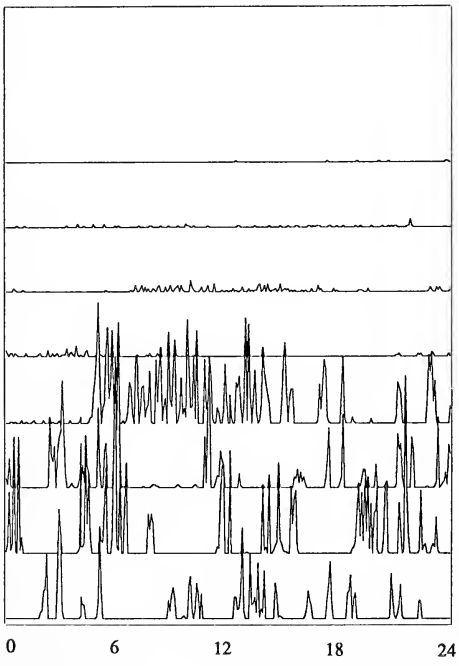


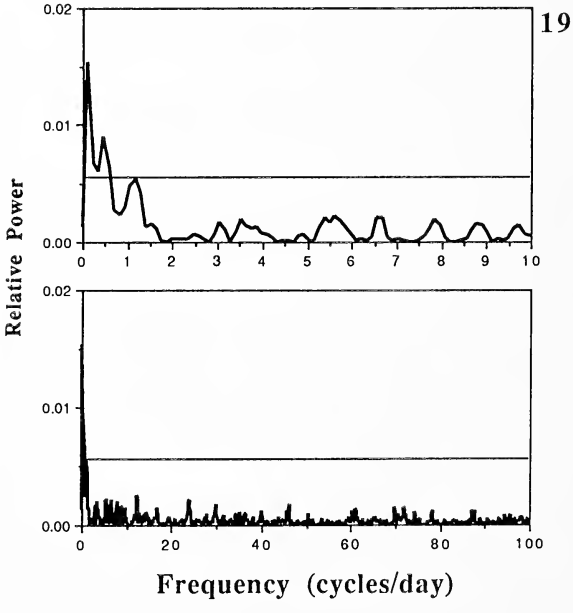


Figures 16–20.—Activity of *A. trigonum* under conditions of constant darkness (DD). See the legend for Figs. 2–8 for an explanation of the layout.









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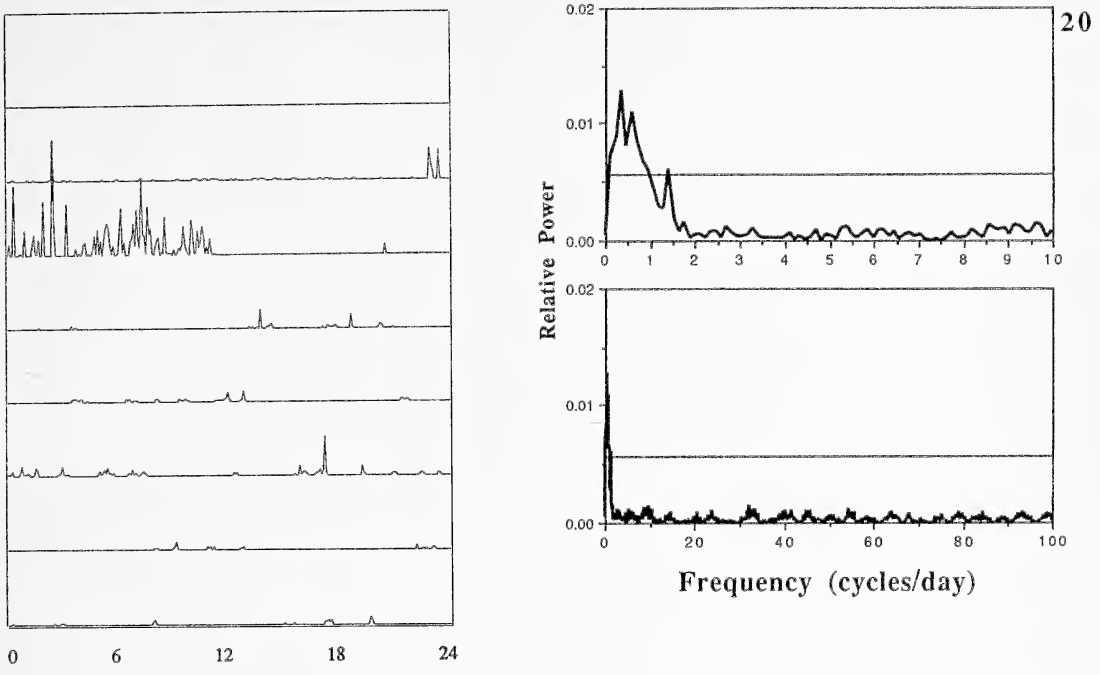


Figures 16–20.—Continued.

of slow rhythms (fewer than 24 cycles per day) activity in each 3-min period was summed and the string of 3-min sums was analyzed by FFT. For the detection of more rapidly cycling rhythms, subsets of the full data string were analyzed without summing (i.e., at 0.625 Hz, one sample every 1.6 s). The two procedures were required because the FFT algorithm could accommodate no more than 4096 data points in a single analysis. (2) Spectral Analysis II: the inactivity periods alone but in order, abstracted from the time-based string above, were analyzed in the same way by FFT and displayed as a power spectrum as described above; this procedure could reveal periodicities in a program which controlled the durations of inactivity periods. For each of the spectral analysis protocols, α was set at 0.01 to decrease the probability of type II errors.

RESULTS

The activity of both species of spiders in the isolation chambers consisted of bouts of nearly continuous activity alternating with periods during which no activity was detectable. Complete activity records for all tested spiders are shown in Figs. 2–20. Presented with each of the activity records in Figs.2–20 are graphs of explained variance as a function of frequency [power spectra, from Spectral Analysis (I)]. In all but one of the graphs that represent spider activity in constant darkness (*F. pyramitela*, Figs. 2–8; *A. trigonum*, Figs. 16–20), significant ($P < 0.01$) peaks occur near 1/day ($1.15 \times 10{-}5$ Hz), an indication that both species should be added to the long list of taxa in which the presence of endogenous circadian rhythms is confirmed. Some of the *F. pyramitela* under LD conditions (Figs. 9–15) were relatively inactive during the light phase of the cycle (Figs. 9–11), but others appeared to be uninfluenced by the dim lighting. The suppression of activity levels in some spiders by relatively dim light suggests that the animals are functionally nocturnal in the field.

Figures 2–20 also show that higher frequency periodicities participate in generating the observed activity patterns. In all of the power spectra, power is concentrated in significant peaks at frequencies between 1 cycle/day and 100 cycles/day: in Fig. 21, which shows cumulative power as a function of frequency for two *F. pyramitela* activity records, 50% of total power is at frequencies below 40 cycles/day and at least 75% is at frequencies below 100 cycles/day. Some of the significant high frequency (i.e., higher frequency than 1/day) periodicities are prominent enough to be easily seen in the activity records themselves. Perhaps the most prominent occurs in Fig. 18 in which a periodicity at about 40

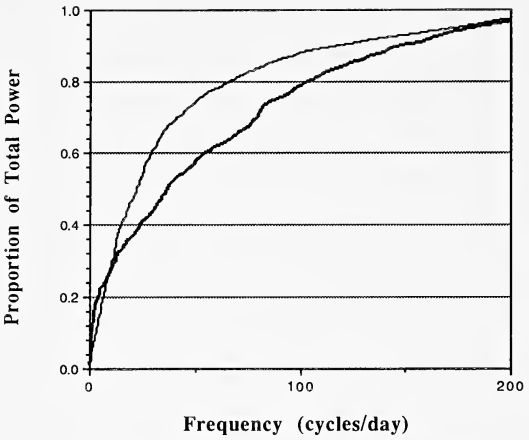


Figure 21.—Cumulative explained variance in the spectral analyses of the activity records of two *F. pyramitela*. The heavy line corresponds to the analysis of the data shown in Fig. 2 and the light line corresponds to the analysis of the data shown in Fig. 7. The most rapid rise in explained variance occurs very near the origin, indicating that high frequencies (> 75 cycles/day) are of minor importance (see text).

cycles/day is evident during the 24 h beginning at 2100 h on day 1, and during day 6. That 24-h period and all of day 6 for the same *A. trigonum* are shown with the corresponding power spectra in Fig. 22.

The intervals between activity bouts for all spiders in DD are shown and analyzed in Figs. 23–34. Spectral Analysis (II) of these intervals alone, kept in order but abstracted from a time-based activity series indicates that in *F. pyramitela* there is no indication of significant periodicity in the patterning of inter-activity intervals: the variance explained by periodicities is distributed relatively evenly across each spectrum of harmonics and is below the 0.01 level of significance for any particular peak above the first harmonic.

DISCUSSION

The behavior of an organism at a particular instant is a function of the interaction between its internal state and information the organism possesses about its surroundings. These two elements are not entirely distinct from each other, however: first, the internal state is in part an evolutionary construct, a consequence of historical responses to the organism's surroundings; and second, the organism's current information about its surroundings is available to it only after filtration through systems of sensation and perception that are sensitive to (and part of) the internal state. In this context, the endogenous rhythms and other behavioral programs of an organism should be seen as parts of the internal

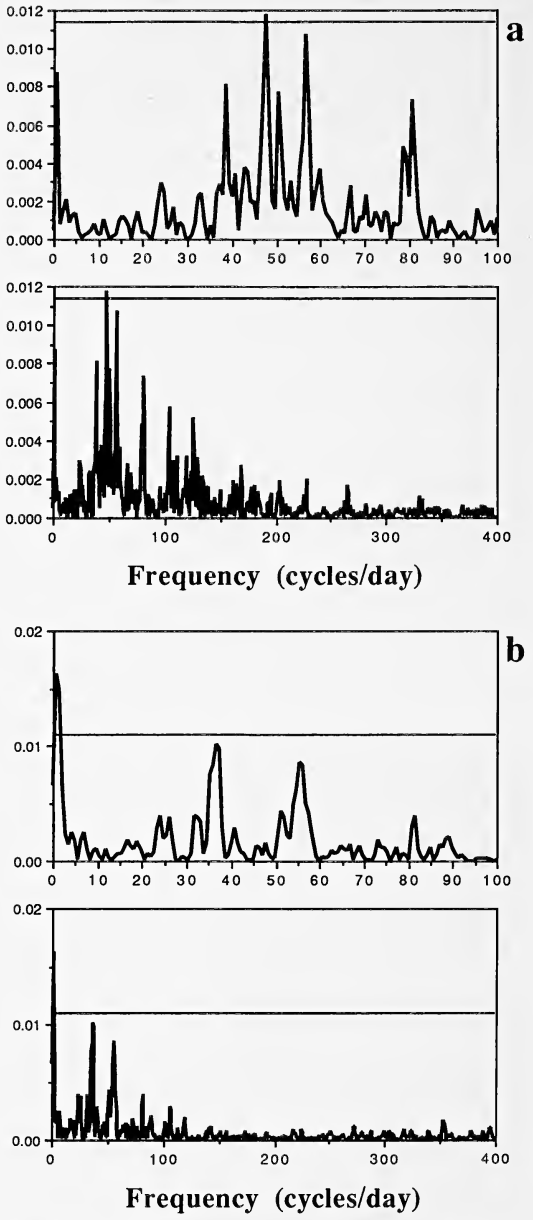
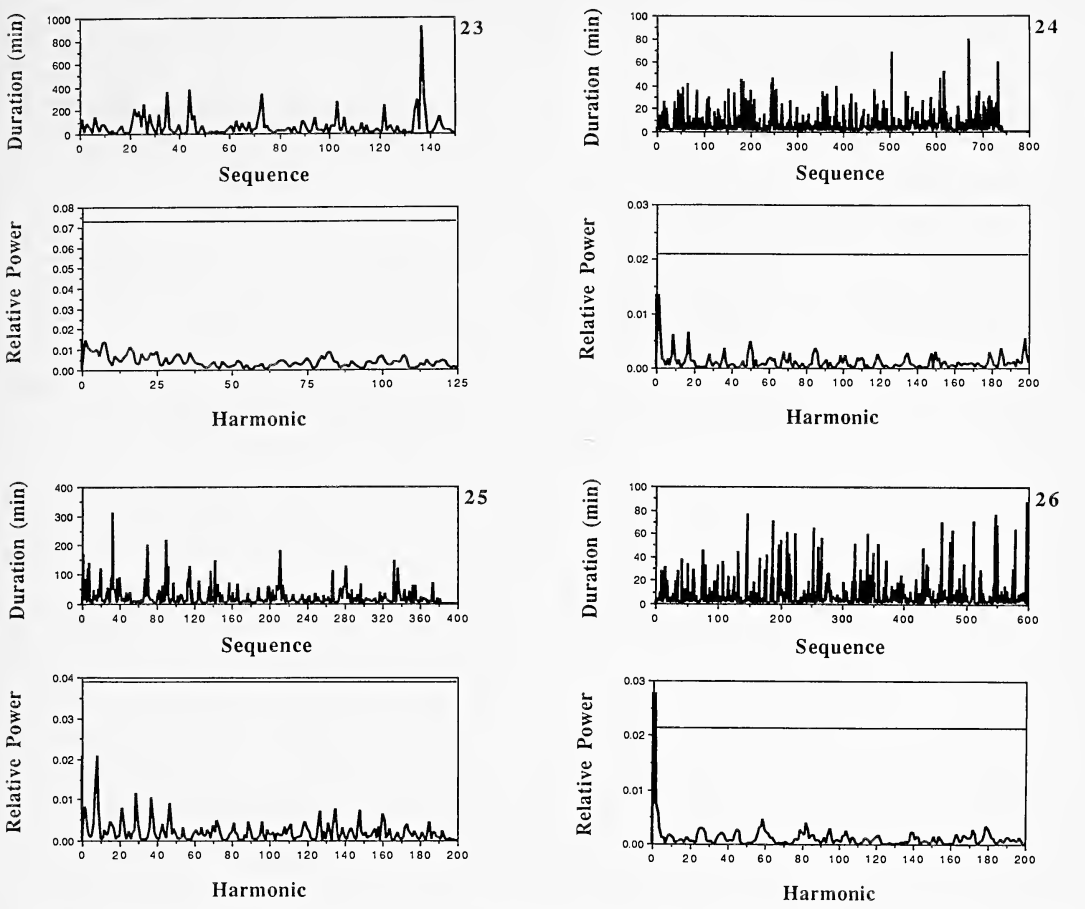


Figure 22.—Power spectra of subsets of the activity data shown in Fig. 18. In that data set, a periodicity at about 40 cycles/day is evident during the 24 h beginning at 2100 h on day 1, and during day 6. The corresponding power spectra are shown here in panels a and b, respectively. As in other power spectra in this study, peaks above the horizontal lines are significant at $\alpha = 0.01$. In panel b, the peak at 36 cycles/day is significant at $\alpha = 0.05$.

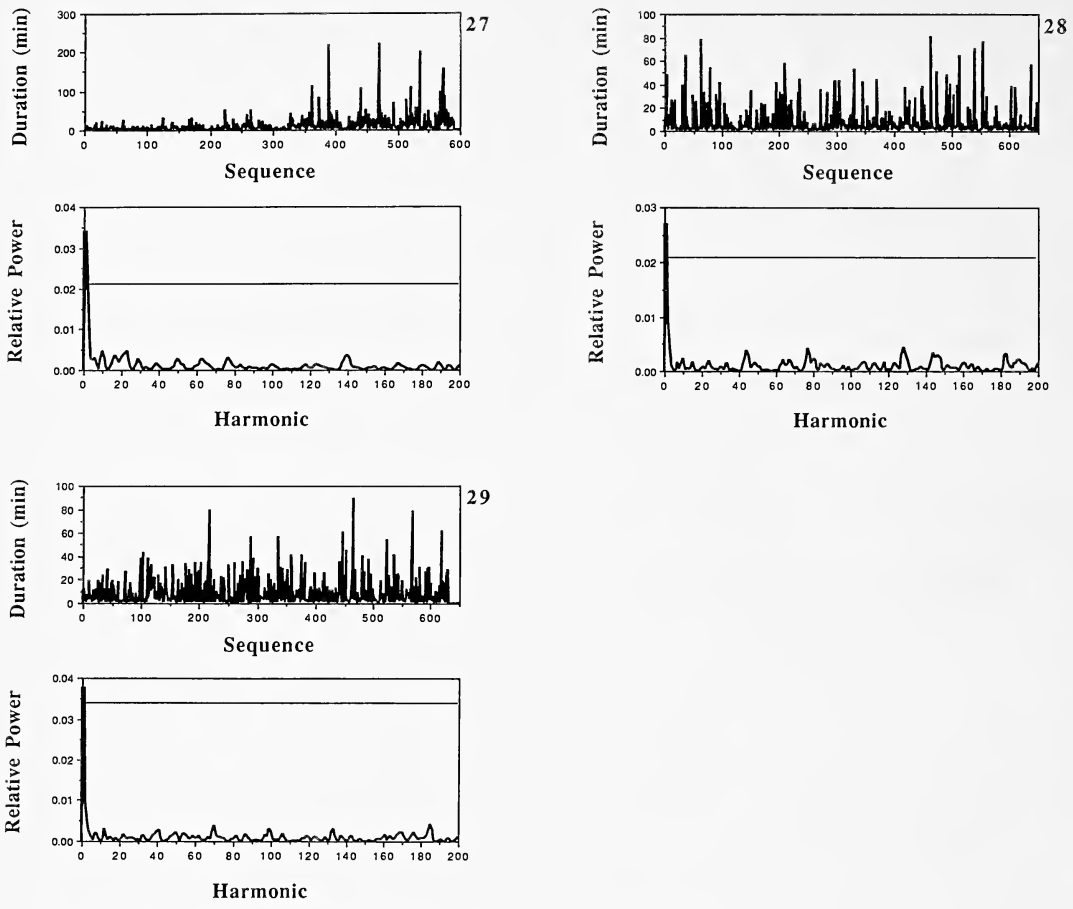


Figures 23–29.—Patterns in the durations of intervals between bouts of activity by *F. pyramitela* in constant darkness (DD). The durations of the intervals themselves, in each figure, are shown (in min) in the top panel, and the power spectrum for that sequence of intervals is shown in the bottom panel. Peaks above the horizontal lines are significant at $\alpha = 0.01$. In none of the analyses was there significant power at harmonics above DC, an indication that the sequences of durations were not different from random.

state that are evolutionary responses to the periodic or probabilistic structure of the environment.

Endogenous rhythms.—The best known endogenous rhythms in nature are those that approximate geophysical rhythms with respect to period length. Their original function was probably to provide a means by which organisms remain synchronized with their environments, and they now function, in addition, in photoperiod measurement and in navigation. Circadian rhythms and other low frequency endogenous rhythms (e.g., circumlunar, circannual) are nearly ubiquitous organizers of activity in organisms. Among spiders, circadian rhythms have been identified (reviewed in Cloudsley-Thompson 1987) but neither higher nor lower frequency rhythms have been implicated in spider behavior. Because most spider species are short-lived, one would not expect to discover among them endogenous rhythms with very long periods (e.g., the lunar month or the solar year). Nor would one necessarily expect to discover endogenous rhythms with very short periods because the environment does not contain biologically important geophysical cycles shorter than the 12.25 h tidal period.

Because of the relatively brief durations of the studies described herein, I could not have demonstrated rhythms with periods longer than about two days. The data do make clear, however, that circadian and higher frequency rhythms in *F. pyramitela* and *A. trigonum* participate in organizing spontaneous motor activity (Figs. 2–20).

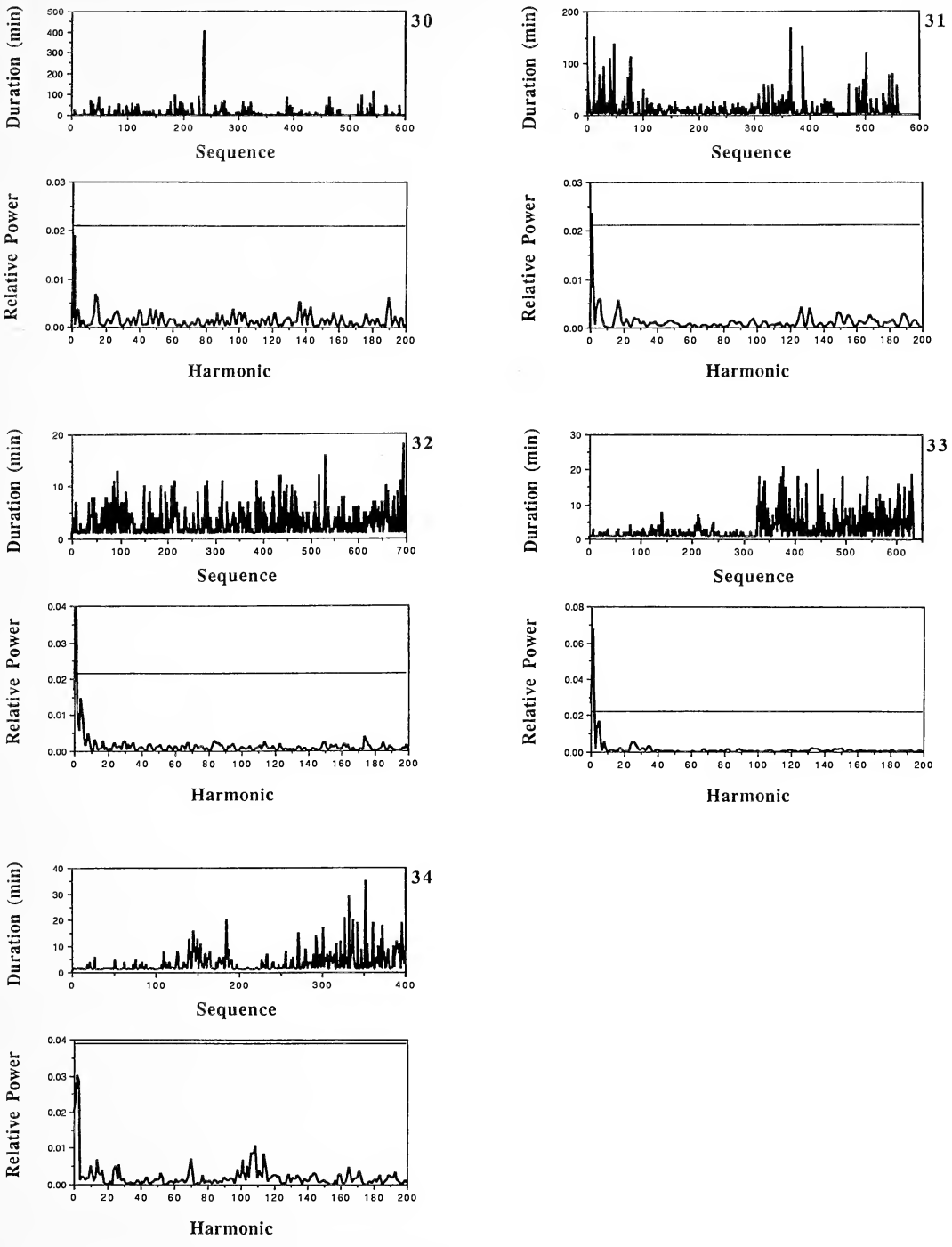


Figures 23–29.—Continued.

The evidence for an endogenous circadian clock is neither surprising nor particularly interesting given the ubiquity of these clocks in biological systems and their obvious efficacy in maintaining synchrony between the organism and its environment. The presence, and in some instances the predominance, of higher frequency rhythms, in contrast, is quite interesting.

Because of the absence of biologically important geophysical cycles with frequencies from 3–100 cycles/day, the significant periodicities in spider motor activity uncovered in that range cannot be of use to the spiders as environmental synchronizers. Moreover, because the spiders in these studies were given neither food nor water, the most likely physiological rhythms (those associated with the filling and emptying of the nutrient and water pools) must be discounted. I am left without a strong hypothesis with which to explain the function(s) of the high frequency periodicities demonstrated in the spontaneous motor activity of these isolated spiders. Of particular interest are the relatively stable oscillations that persist for many cycles and appear to be stable after several days (e.g., Figs. 18, 22): these are likely to be both important in the lives of the spiders and amenable to experimental investigation.

Other behavioral programs.—The periodicities described above are time-based; that is, they are detected as peaks of activity which are repeated at regular intervals in the time domain. Quite a distinct type of behavioral program would be one that obeyed the following algorithm: when behavior x begins, continue x until t seconds have elapsed, then begin behavior y; assign t a new value based on some specified trigonometric function; repeat. The resulting periodicity in the durations of x would be undetectable if there were uncorrelated variability in the durations of



Figures 30–34.—Patterns in the durations of intervals between bouts of activity by *A. trigonum* in constant darkness (DD). See the legend to Figs. 23–29 for details of the layout. In none of the analyses was there significant power at harmonics above DC, an indication that the sequences of durations were not different from random.

y. For example: suppose *y* is motor activity and *x* is inactivity; if activity occurs in bouts that vary in duration according to some non-periodic function, then peaks in the durations of inactivity bouts would appear nonperiodic; if, in contrast, inactivity bouts were extracted in order from the time series, the periodicity of peaks in the durations of inactivity bouts would become apparent. This is the reasoning behind Spectral Analysis II. In the linyphiid spider, *F. pyramitela*, and in the theridiid spider, *A. trigonum*, the durations of inactivity bouts show no evidence of periodicity (Figs. 23–34) which leads to the conclusion that these bouts are not generated by the sort of behavioral program outlined above.

Thus there is no evidence from the data presented here that the inactivity bouts of *F. pyramitela* and *A. trigonum* are regulated by any sort of non-random program. What, then, determines the duration of a particular period of inactivity in these spiders? The possibility that they are coupled to, or driven by, some process the output of which is itself random is intriguing but well outside the scope of this study.

Conclusion.—My analysis of the motor activity patterns of *F. pyramitela* and *A. trigonum* reveals that endogenous oscillators participate in determining the timing of activity but not the durations of inter-activity intervals. Some nonperiodic processes, which may be the equivalent of random-number generators, are also important in determining the durations of inter-activity intervals. Both the nonperiodic processes and the endogenous oscillators with periods much shorter than 24 h are particularly interesting because they constitute an unexplored set of behavioral programs that may influence much of the behavior of these spiders.

ACKNOWLEDGMENTS

I am indebted to Steve Clark (at Vassar College) and Jeff Cynx (at The Rockefeller University) for several of the conversations that led to this study, to Thomas Getty (at Michigan State University) for his helpful comments on the analysis of apparent noise, and to Tim Forrest (at the National Center for Physical Acoustics) for his guidance in the use of the discrete Fourier transform.

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PREDATION BY SPIDERS ON GROUND-RELEASED SCREWWORM FLIES, *COCHLIOMYIA HOMINIVORAX* (DIPTERA: CALLIPHORIDAE) IN A MOUNTAINOUS AREA OF SOUTHERN MEXICO[1]

John B. Welch[2]: Screwworm Research, Agricultural Research Service, United States Department of Agriculture, Tuxtla Gutierrez, Chiapas, Mexico

ABSTRACT. Predation by spiders on ground-released adult screwworms, *Cochliomyia hominivorax* (Coquerel), was studied near Tuxtla Gutierrez, Chiapas, Mexico, during 13 August 1984–23 January 1985. Observations of predatory behavior and manual collections of spiders during September provided the majority of the data. Species in 12 genera of spiders were confirmed as predators of screwworm flies. *Nephila clavipes*, *Eriophora ravilla*, *Neoscona oaxacensis* and *Leucauge* spp. were the most important predators. Spiders caused an estimated 4.5% mortality to flies in a 2250 m^3 area during September. Capture of screwworm flies in webs up to 10 m above ground suggests the need to investigate the importance of forest canopies in screwworm ecology.

The screwworm fly, *Cochliomyia hominivorax* (Coquerel), native to the western hemisphere, is an obligate parasite of warmblooded animals. Studies of the ecology of screwworms in the tropics have been conducted since the late 1970's (e.g., Krafsur et al. 1979; Spencer et al. 1981; Brenner 1985; Mangan & Thomas 1989). However, information on predation of screwworms is generally lacking.

My interest in predation of screwworms began during an unpublished study of dispersal of ground-released adult screwworm flies in a mountainous area of southern Mexico. On the occasions of the first two releases of flies (22 May and 6 July 1984), spider populations were apparently low because few spiders and webs were seen during the collection of the fly samples. Numerous spiders and webs were encountered during trips to the study area the week before the planned third release (14 August). Spiders continued to be numerous prior to the fourth release (25 September). Spider populations appeared to decline after this release, as few spiders and webs were observed while collecting fly samples during the fifth and sixth releases (13 November 1984 and 22 January 1985).

The results of an investigation into predation on adult screwworm flies during the third and fourth releases are presented herein. Additional data concerning spider predation during the fifth and sixth releases and other screwworm fly dispersal studies are included. Information on the predatory behavior of spiders is also presented.

METHODS

The study was conducted in the Sumidero Canyon National Park located *ca.* 15 km north of Tuxtla Gutierrez, Chiapas, Mexico. Spiders were also collected from Finca San Rafael, a study site *ca.* 32 km south of Tuxtla Gutierrez during another trapping study of *C. hominivorax* (Welch 1988).

The study site in the Sumidero Canyon National Park was located on the southern face of the mountain at an elevation of *ca.* 1040 m above mean sea level. The habitat was a low deciduous forest (Miranda 1975) comprised predominantly of trees *ca.* 3–8 m tall, with scattered, emergent trees above the canopy. The study site at Finca San Rafael was also situated in a low deciduous forest, although the trees were taller (ca. 4–10 m) and the vegetation was more dense.

Sterile screwworm pupae of the A-82 strain obtained from the sterile-fly production plant of the Joint Mexico-U. S. Commission for the Eradication of Screwworms were placed in the field on 25 September (and the other release dates) and allowed to emerge. Pupae were marked with 20 g/liter of fluorescent powder (Dayglo Color, Cleveland, Ohio) and distributed in open card-

[1] Mention of a proprietary product does not imply an endorsement or a recommendation for its use by USDA.

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board cartons (1.45 × 18 × 4 cm; 0.5 liter/carton) stacked inside a wooden crate (26.5 × 36 × 49.5 cm). The crate was covered with a corrugated tar-paper roof for protection and suspended 1.5 m above ground by wire from a tree limb. This is termed "ground-released" as opposed to being released from an airplane. Percentage of emergence was determined from controls (0.5 liter carton of marked pupae enclosed within a screen bag inside the release crate) (Welch 1988). All flies were examined under longwave ultraviolet light for fluorescent markings on the frontal suture (Brenner 1984).

Predation data were obtained by direct observation and by collection of spider and fly samples. Spider and fly activities were monitored visually at the Sumidero release site 5 from 0630 to 1600 h (time period due to park hours) on 26 and 27 September. Three pitfall traps filled with 70% ethyl alcohol were operated from 25–29 September, 13–17 November, and 22–26 January. Fly emergence ended and manual collections of spiders and sweep samples of the vegetation in the vicinity of release site 5 were conducted on 28 September. Spiders with screwworm flies in their webs were also collected from other release and trap sites within the Sumidero Canyon National Park and Finca San Rafael throughout the remainder of the study period.

A search for screwworm fly cadavers and spiders was made along a transect (150 m) heading south of release site 5 on 28 September. The transect was located along an existing trail descending the mountain because cutting of new trails or paths within the park was prohibited.

Specimens were sent to William B. Peck for identification. Voucher specimens are maintained in a collection at the United States Department of Agriculture, Agricultural Research Service, Screwworm Research Laboratory at El Alto de Ochomogo near San Jose, Costa Rica (as is typical in Costa Rica, the actual laboratory site has no street or mailing address; requests for information concerning the voucher specimens should be directed to the author at his listed mailing address).

RESULTS

A total of 126 spiders representing 12 families and *ca.* 26 species were collected during this study. Most (78.6%) of the spiders belonged to the families Tetragnathidae and Araneidae, with *Nephila clavipes* L., *Leucauge* spp., *Neoscona oaxacensis* (Keyserling) and *Eriophora ravilla* (C. L. Koch) accounting for 19.0, 19.0, 14.3, and 13.5% of the total spiders collected, respectively. Other araneid genera included *Micrathena*, *Verrucosa*, and *Mangora*. Spiders belonging to the families Filistatidae, Tengellidae (*Zorocrates*), Plectreuridae (*Plectreurys*), Theridiidae (*Argyrodes*), Lycosidae (*Lycosa*), Oxyopidae (*Peucetia*), Clubionidae, Sparassidae, Selenopidae (*Selenops*), Thomisidae (*Misumenoides*, *Misumenops*) and Salticidae (*Phidippus*) were also collected. The majority (103 specimens, 7 families) of the spiders collected were captured manually, while 5 specimens representing 4 families were collected by pitfall trap, and 18 specimens representing 3 families were collected by sweep sample.

Predation by spiders on screwworms was evidenced by dead flies in the webs of spiders (Table 1) and by direct observation of flies being captured. Species of *Misumenops* sp. and *Misumenoides* sp. were collected, each with one screwworm fly. Additionally, a *Peucetia viridans* (Hentz) was discovered with two dead flies on one occasion. Species of 11 genera of spiders captured screwworm flies in webs during the study. The four most commonly collected groups of spiders listed above also accounted for the most (91.5%) webs containing screwworm flies (Table 1). Webs of *N. clavipes* accounted for 43.9% of those with ensnared flies. *Eriophora ravilla*, *N. oaxacensis*, and *Leucauge* spp. webs accounted for 19.0, 17.8 and 9.5%, respectively, of the webs with flies. All webs of *N. clavipes* and 88.9 and 93.7% of webs of *E. ravilla* and *N. oaxacensis*, respectively, contained screwworm fly cadavers. Only 40.0% of the webs of *Leucauge* spp. contained dead flies.

A rough estimate of percent predation of screwworms may be obtained from the collections of data along the transect heading south of the release crate at release site 5. A total of 389 screwworm flies were observed in webs along the transect within 75 m of the release crate. Webs were located within *ca.* 3 m of the transect and up to 10 m above the ground. Based on emergence of controls, an estimated 8710 flies were released from the site, thus resulting in a calculation of 4.5% mortality of flies by spiders within the 2250 m^3 area of the transect. Inspection of the surrounding area resulted in few additional webs being located and no screwworms were seen in the webs. Therefore, the estimate would only be valid for the area of the transect; and it is still imprecise because flies killed and removed from the webs, and flies that were bitten and escaped

from the web, but then died, etc. were not counted.

Although not along the transect, a fly released from site 1 got caught in a web of *N. oaxacensis* located 150 m to the south, the record distance between release site and point of entanglement in a spider web during this study.

Due to the small sample size, fly capture data were pooled for all spider species. Generally, more flies per web were ensnared from 1–10 m from the release crate than from 11–20+ m for most species of spiders (Fig. 1). Most webs of all species (64.6%) along the transect were 1–3 m above ground and accounted for the most screwworm flies ensnared. More webs (27.7%) were 7–10 m than 3.5–6.5 m above ground (7.7%), and more flies were caught in the higher webs than those located within the 3.5–6.5 m range (Fig. 2). This pattern was exhibited by *N. clavipes* and *E. ravilla* webs. Entanglement in webs of *Neoscona oaxacensis* occurred 1–3 m above ground, and the webs of the unidentified species were mostly 1–3 m above ground.

Observations of fly activity at the release site indicated that flies began leaving the release crate at 0800 h on 26 September and continued until observations were stopped at 1600 h. Fly activity began at 0637 h on 27 September and continued until 1437 h, at which time dispersal from the release crate was complete. On both days, fly activity increased when direct sunlight reached the release crate, and slowly decreased when direct sunlight was blocked by clouds. No flies left the release crate while it rained, and flies outside of the release crate moved to the undersides of leaves and rocks during the rain.

Observations on the predatory activity of spiders in webs within three m of the release crate were made in relation to screwworm flies emerging from the release crate at release site 5. Individuals of *N. clavipes* (five females) began feeding on the flies immediately as the flies became trapped in the webs on the morning of 26 September. This activity continued from 0800 h until *ca.* 1020 h, when the spiders began repairing the webs. Predation and web repair continued throughout the afternoon while the flies were active. However, spiders began ignoring some of the new flies caught in the webs *ca.* midday (e.g., one spider with 29 flies in its web began ignoring the flies at 1148 h and another spider with 14 flies in its web began ignoring other flies at 1151 h). Flies that were ignored and not killed immediately had time to make a possible escape.

Table 1.—Species of spiders and number of webs containing at least one cadaver of *Cochliomyia hominivorax* after field release. Cadavers also were found in the webs of an unidentified theridiid and other unidentified species.

Species	Number of webs	
	With prey	Without prey
Plectreurys sp.	1	0
Argyrodes sp.	1	3
Araneus sp.	1	0
Eriophora ravilla	16	2
Nephila clavipes	36	0
Micrathena spp.	2	2
Verrucosa arenata	2	0
Neoscona oaxacensis	15	1
Leucauge spp.	8	12
Total	82	20

Approximately 27.5% (19 of the 69) of the flies caught in the webs of *N. clavipes* escaped during the study period on 26 September.

At 1420 h, a female *E. ravilla* climbed onto a web of a female *N. clavipes*, and the *N. clavipes* rapidly retreated to the vegetation to which the web was anchored. The *E. ravilla* began examining the dead flies (11) in the web and initiated repairs to the web. After repairs were completed, the spider began preying on newly captured flies and maintained the web for the remainder of the afternoon. Upon my arrival at the study site on the morning of 27 September, the female *E. ravilla* had vacated the web, and what appeared to be the original *N. clavipes* owner (based on size and appearance) had returned and was repairing the web. This specimen continued predation in the web and the *E. ravilla* did not return.

The web of the largest female *N. clavipes* had not been repaired by the morning of 27 September, had several large holes and was cluttered with the corpses of flies. This individual made no attempt to repair the web and did not react to any new flies hitting her web during the day. All of the flies that were caught in her web on 27 September escaped.

The percentage of flies escaping the webs of *N. clavipes* on 27 September could not be estimated because the numbers of flies that were hitting the webs and escaping were too numerous to count. At one point during the morning (0745 h), during peak dispersal of the flies, it was estimated that *ca.* 40 flies per minute were hitting the webs.

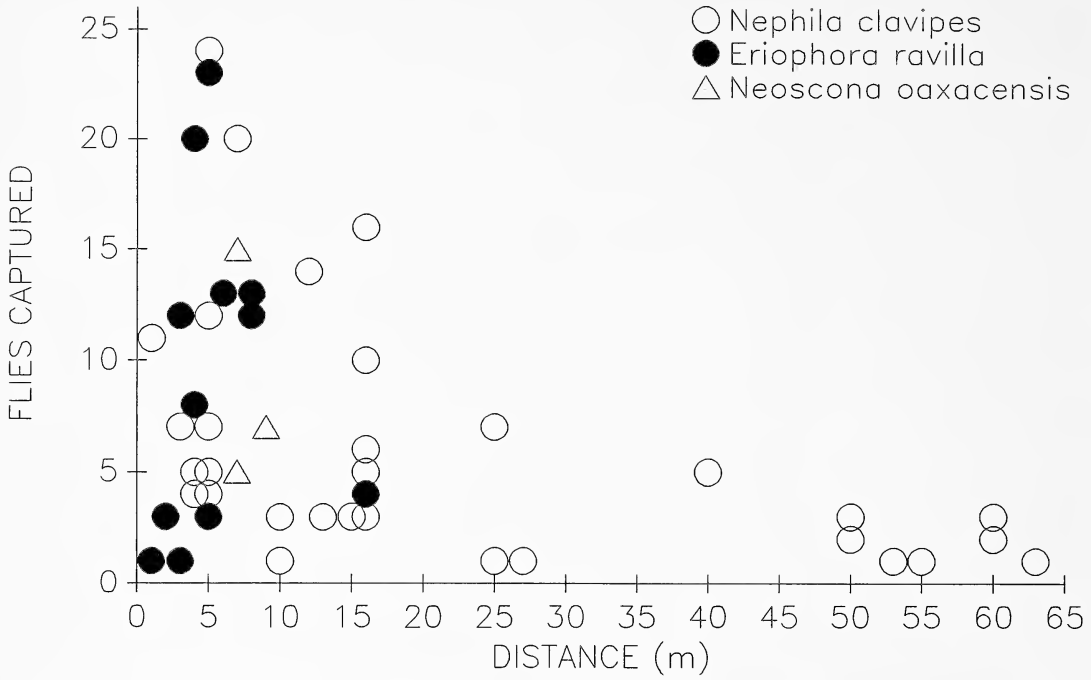

Figure 1.—Number of screwworm fly cadavers found in webs of three species of spiders located from 1–75 m from the release box.

Nineteen screwworm flies were observed being preyed upon during the hours of 0655–1130 by *N. clavipes*.

Observations on the predation activity of eight female *E. ravilla* were made in relation to the release crate at release site 5. Predation activity of *E. ravilla* also began on the morning of 26 September when the dispersing screwworm flies began hitting the webs. At first, webs were repaired immediately after the flies were killed and removed. However, beginning around 1020 h, the spiders ceased repairing the webs. Then at 1108 h some individuals of this species began ignoring live flies entangled in their webs. Flies were ensnared and killed throughout the day until observations were stopped at 1600 h.

A total of 88 screwworm flies was ensnared in webs of *E. ravilla* on 26 September. Seventeen flies escaped from the webs, resulting in an estimated 19.3% escape.

Although more flies were dispersing on 27 September, *E. ravilla* began ignoring the flies hitting the webs after 0848 h. Three of seven screwworm flies ensnared before 0848 h escaped, resulting in an estimated 42.9% escape for that time period.

Predation of screwworm flies dispersing from the release crate at release site 5 by three female *N. oaxacensis* showed the same pattern as that by *N. clavipes* and *E. ravilla*. Predation on 26 September began immediately when the flies began hitting the webs and continued until 1530 h. Flies began escaping from the webs at 1035 h with an overall 12.7% escape (7 of 55). Spiders also began repairing their webs around 1020 h.

Most of the flies caught in the webs of *N. oaxacensis* on 26 September had been removed by 0630 h on 27 September. Ensnarement of flies on 27 September began at 0654 h and continued until 1000 h. Two flies escaped during that time period, resulting in 11.8% escape.

DISCUSSION

Predation of screwworm flies by species of 12 genera of spiders was observed in this study. Specimens of *E. ravilla*, *N. clavipes*, *N. oaxacensis*, *V. arenata* and *P. viridans* were the only spiders within these genera identified to species, with the first three being the most important predators.

Nephila clavipes apparently build their webs in areas within the forests which are probable flight paths of insects (Robinson & Mirick 1971). Collections of flies in webs up to 10 m above the

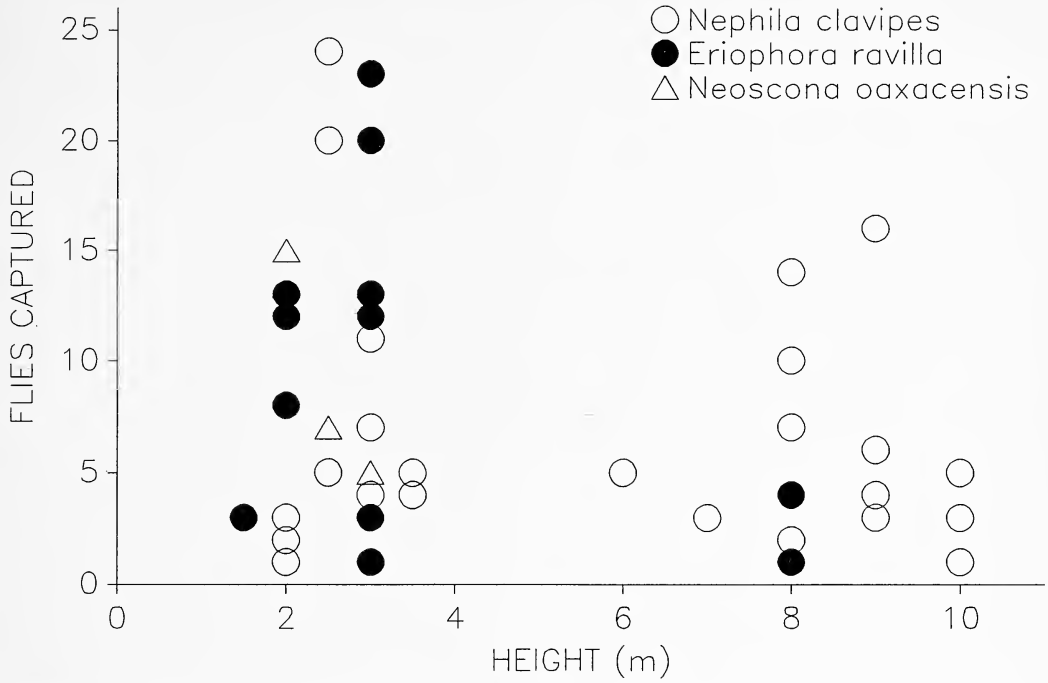

Figure 2.—Number of screwworm fly cadavers found in webs of three species of spiders from 0.5–10 m above the ground.

ground, in the area of the forest canopy, suggest that the forest canopy may be important to the ecology of screwworms. More screwworm flies have been collected in forest habitats than in pastures (Mangan & Thomas 1989). Studies of screwworms have been confined to ground level, so further investigations of the vertical distribution of screwworms in relation to habitat are needed.

The predatory behavior exhibited by the *N. clavipes* under observation agrees with the descriptions in the literature with one major difference. It was reported that *N. clavipes* always transported its prey to the hub of the web after immobilization (Robinson et al. 1969; Robinson & Mirick 1971). None of the five female *N. clavipes* that were monitored at release site 5 in my study exhibited this behavior: flies were never moved from the site of capture. Initially, when prey numbers were low, an immobilization bite was given and wrapping occurred at the capture site followed by apparent feeding on the prey *in situ*. When large numbers of flies were hitting the webs or when the spiders apparently became satiated, post-immobilization wrapping was omitted. The latter is in agreement with Robinson et al. (1969) and Robinson & Mirick (1971). This apparent feeding may have been what was referred to as a "long bite" by Robinson & Mirick (1971); however, because considerable time was spent by the spiders with the prey and later prey were ignored (suggesting the spiders' hunger was satiated), it appeared that the spiders were feeding. Upon my return to release site 5 on 27 September, corpses of flies were still present at the site of capture in the webs and none were present at the hub where the spiders were resting. Also, the bite and back-off behavior described by Robinson & Mirick (1971) was not exhibited by *N. clavipes* during my study, but this was probably due to the smaller size of the prey (i. e., flies *vs.* crickets) between the two studies.

Differences in percentages of prey escaping from *N. clavipes* webs between earlier studies and mine were probably due primarily to the unusually high density of screwworm flies in the area. An estimated 27.5% of the screwworm flies escaped from the webs on 26 September. Robinson et al. (1969) reported that 46% of the stingless bees (*Trigona* sp.) ensnared, escaped from the webs, primarily while *N. clavipes* was occupied at the hub of the web. However, no estimation was calculated for 27 September because too many flies to be counted were hitting the webs and were being ignored because the spiders were apparently satiated.

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THE NATURAL HISTORY OF THE CALIFORNIA TURRET SPIDER *ATYPOIDES RIVERSI* (ARANEAE, ANTRODIAETIDAE): DEMOGRAPHICS, GROWTH RATES, SURVIVORSHIP, AND LONGEVITY

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ABSTRACT. A large and dense population of over 500 burrows of *Atypoides riversi* in a 2.0 × 3.2 m area was monitored for two years to indirectly determine demographics, growth rates, survivorship and longevity of the spiders. Twelve size classes of spiders were designated by correlating spider size to burrow size. All size classes were present simultaneously throughout the year. Variable growth rates were recorded for spiders in each size class, and survivorship was lowest for spiders in the smallest size classes. It is estimated, based in large part on growth rates, that *A. riversi* can live at least 16 years in the field.

The only long term comprehensive study of the genealogy and demography of a large population of mygalomorph spiders concerns the Australian ctenizid *Anidiops villosus* (Rainbow) (Main 1978). In another study, Marples & Marples (1972) observed a population of several species of New Zealand ctenizids for six years. The demographics of burrowing wolf spiders have been examined in detail by McQueen (1978, 1983), Humphreys (1976) and Miller & Miller (1991).

Herein I describe the natural history of the fossorial mygalomorph spider *Atypoides riversi* O. P- Cambridge, the California turret building spider (Rivers 1892). Unlike the long term field studies of Main and the Marples, my objectives were to determine, in a two-year period, the demographics, growth rate, survivorship, and longevity of *A. riversi*. Unlike Main (1978) and Marples & Marples (1972), who measured burrow and door diameters but did not correlate these measurements to spider size, I measured and correlated burrow entrance size to spider size. McQueen (1978), Humphreys (1976) and Miller & Miller (1984) found positive correlations for certain burrowing wolf spiders. Decae et al. (1982), studying the burrow structure of a ctenizid, also found a positive correlation between carapace length and burrow diameter but did not associate this with longevity. Using the correlation and following all burrow size changes through the two year period, I derived life history information comparable to following a single cohort of *A. riversi* through its long life. Miller & Miller (1991) used a similar approach to study *Geolycosa turricola*.

Additional natural history information on various antrodiaetids can be found in Atkinson (1886a, 1886b), Coyle (1971, 1986), Rivers (1891), Smith (1908), Vincent (1980, 1985, 1986), and Vincent & Rack (1982).

METHODS

Study sites.—Two study sites at the University of California's Blodgett Forest Research Station, located in the American River watershed on the western slope of the Sierra Nevada in El Dorado County, approximately 10 miles west of Georgetown and at an elevation 1275 m were chosen for their high density of burrows and uniform ground cover. The population dynamics of spiders in both areas were similar; therefore, this paper reports on only one. Population data for the other study area and vegetation descriptions for both are in Vincent (1980).

The study site measured 2.0 × 3.2 m and consisted of 160 20 cm square quadrats formed by a grid system composed of nylon string and wooden stakes. The stakes were placed at 20 cm increments around the perimeter of the plot, and string was placed on or slightly above the ground connecting facing stakes. Ground cover was mostly pine and cedar needles with occasional pine seedlings present during the spring and summer months. A barbed-wire fence enclosed the study area to exclude deer and other large animals.

Correlation of spider size and burrow entrance size.—A series of 15 non-metric ball bearings ranging in diameter from 2/32 inch (1.59 mm) to 16/32 inch (12.7 mm) in increments of 1/32 inch (0.79 mm) were hard-soldered to thin single fiber wire "handles". These ball bearings were then used to measure the internal diameter of spider burrow entrances. The internal diameter was considered equivalent to the diameter of the ball bearing that fit (or came the closest to fitting) the narrowest section of the tapered burrow entrance. For convenience, burrow size classes were designated by the numerators that fit the entrances (sizes 2–16). Attempts to measure burrow entrances accurately with a caliper or ruler proved to be difficult and damaging to the flexible and fragile entrance.

Six to 14 burrows ($n = 128$) representing each size class were arbitrarily chosen near the study site for measurement (Vincent 1980). After each burrow was measured, the resident spider was dug from its burrow, anesthetized by cooling with crushed ice (large spiders) or CO_2 (small spiders), and measured. Spiders were measured with a stereomicroscope fitted with an ocular micrometer accurate to 0.039 mm. Measurements of maximum width of both the carapace and sternum were correlated to the internal diameter of the burrow entrance.

Observation platform.—A portable observation platform consisting of a 2 × 1.33 m sheet of plywood was supported approximately 12 cm over the plot by planks and blocks. The leading edge of the platform coincided with the trailing edge of the row being examined to allow a detailed view of one 20 cm square quadrat. After examining all quadrats in a row, I advanced the platform to the trailing edge of the next row, etc. Since *A. riversi*, like some other fossorial mygalomorphs, is sensitive to vibrations, successful observations necessitated moving slowly on the platform. Adjusting the platform caused some spiders to retreat temporarily down their burrows.

Burrow observations.—The position of each burrow was noted and its entrance diameter was measured. Burrows with flexible and freshly silked turrets were measured for size class designation. The following burrow conditions were recorded: (1) occupied [spider was seen in its burrow]; (2) abandoned [burrow appeared in use, but no spider was detected during the immediate observation period, approximately five minutes]; (3) closed [entrance was folded closed and sealed with silk]; (4) missing [burrow could not be found]; (5) old [burrow was in a state of disrepair, the turret was stiff and/or torn or non-existent]. These and other relatively rare burrow conditions are discussed in detail in Vincent (1980).

Data collection dates.—Burrows were initially censused 5–23 September 1976. On 22–24 April 1977 new burrows and burrow conditions for a random sample ($n = 153$) of previously censused burrows of sizes 3 through 11 were recorded. Also, burrow conditions for all burrows of sizes 12, 13, and 14 were recorded ($n = 13$). The random-sample size for each size class was determined so that the standard deviation of the estimated proportion would be no greater than 0.30. Confidence intervals for the true proportions were calculated by a formula given in Bickel & Daksun (1977, formula 5.1.13), and modified to account for sampling without replacement (Cochran 1977, sec. 2.15). During 28–31 July 1977, new burrows were mapped and recorded, and previously recorded burrows were measured again. On 20 August 1977 a random sample of burrows present on 28–31 July, 1977 was censused to confirm the presence of spiders in the burrows previously sized. Sample size and confidence intervals were determined as above for the April 1977 random sample. All burrows present on 28–31 July 1977 were recensused 19–20 May 1978 to see if they contained spiders. Burrows that contained spiders on 19–20 May 1978 were recensused and remeasured 3–6 August 1978, and all burrows in odd-numbered rows were observed at night with a dim unfiltered flashlight as a further check on spider presence. If a spider was not immediately visible in its burrow, I waited several minutes for it to appear; if it still did not appear, I considered the burrow abandoned. Again, all new burrows were recorded and mapped.

Survivorship calculations.—Survivorship of *A. riversi* was indirectly determined by subtracting from the initial number of burrows censused the number of burrows missing or considered "old" during each consecutive census. Survivorship of eggs and emerging spiderlings is unknown.

RESULTS AND DISCUSSION

Correlation of spider size and burrow entrance size.—Burrow entrances ranged from 3/32 inch (2.38 mm) through 14/32 inch (11.06 mm). A regression of spider size (carapace widths) against burrow entrance size was highly significant ($P < 0.001$) (Fig. 1).

Assumptions.—In estimating the following

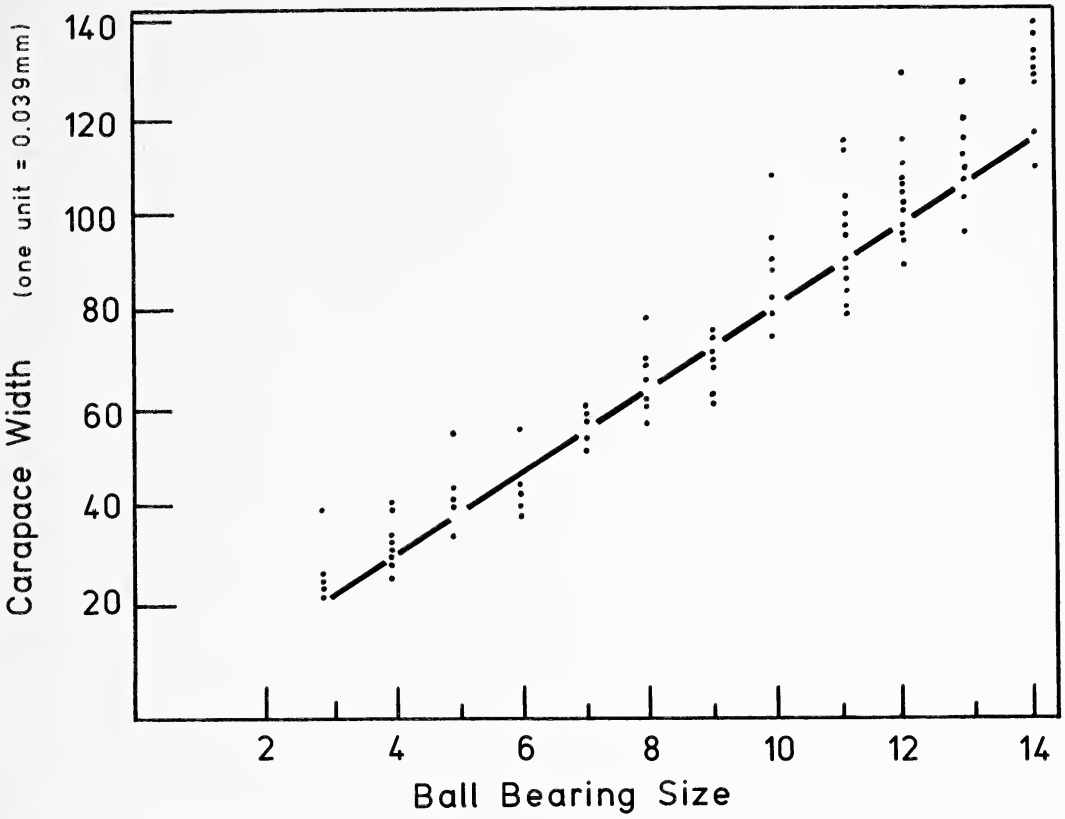

Figure 1.—Regression of ball bearing size on carapace width ($Y = 8.3X - 3.1$, $R^2 = 0.934$, $P < 0.001$).

demographics, survivorship, growth rates and longevity for *A. riversi*, I assume each burrow has had only one occupant who had enlarged and maintained it over time, that burrows present and in good shape contain a living spider, and that missing burrows are a measure of spider mortality.

Various field observations support the assumption of "burrow fidelity". Throughout most of the year I have measured increases in burrow width for all size classes and have often observed excavated soil adjacent to burrows. Further, during hundreds of hours of observing *A. riversi* in the field, only on one occasion was a spider seen totally outside its burrow. (This spider was later found to be parasitized by a nematode). Indeed, the reluctance of *A. riversi* to leave their burrows was evident by the difficulty encountered in coaxing them completely out even with tethered prey; once outside, they rapidly find their way back to their burrow. Additionally, I excavated hundreds of burrows but never found more than one spider in a burrow. Lastly, pitfall traps placed adjacent to or within 25 m of the study sites, during most of 1977, recovered only adult male spiders and only during the fall mating season.

The above observations suggest that *A. riversi* does not leave its burrow to enter another burrow to evict its resident in a competitive interaction (as in Riechert 1978), to search out larger vacated burrows, or to establish new burrows in better areas. Other antrodiaetids (F. A. Coyle & W. Icenogle pers. comm.), all door-building ctenizids (B. Y. Main pers. comm.; Decae et al. 1982), and a burrow-dwelling theraphosid (Kotzman 1990) apparently maintain the same burrow throughout life.

The assumption that burrows which were maintained contained spiders (deteriorated burrows rarely did) was based in part on a 5 August 1978 evening census in which 97.3% of the maintained burrows ($n = 263$) were occupied by spiders. Those burrows in which a spider was not observed at the entrance may still have contained a spider at the bottom, perhaps feeding or repelled by my dim flashlight.

The last assumption equating missing burrows with spider mortality may not be entirely accu-

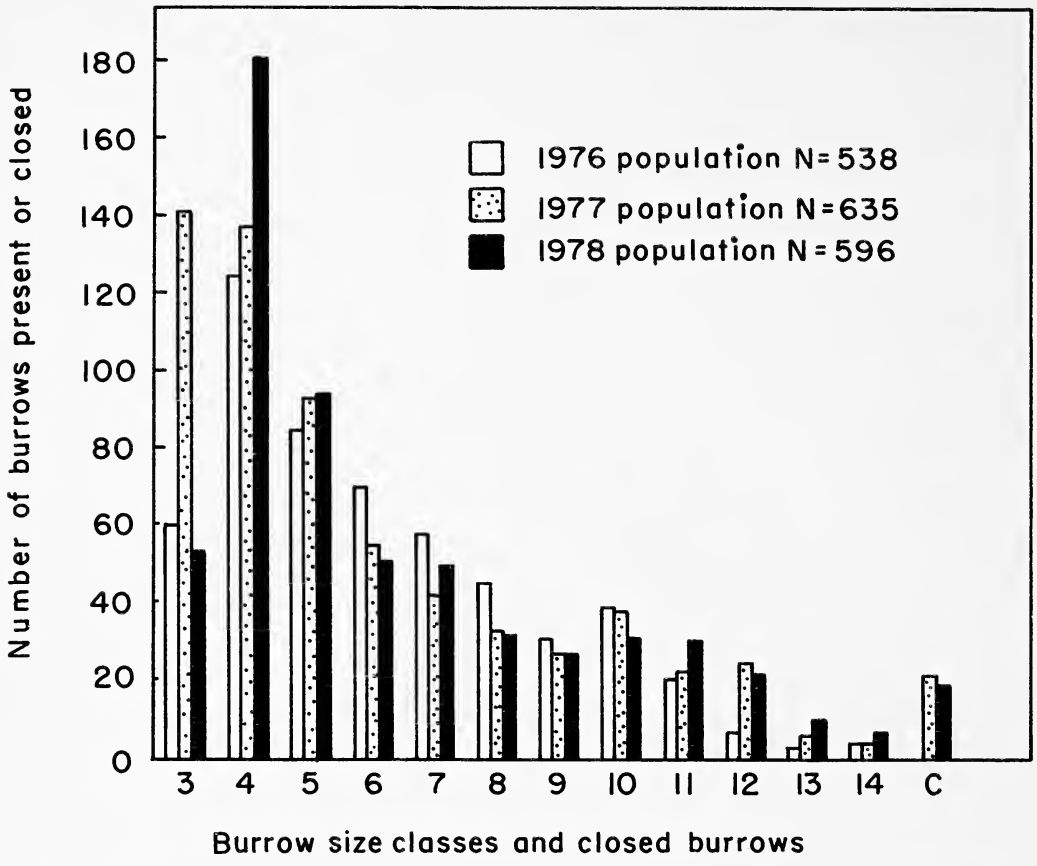

Figure 2.—The number of occupied and closed burrows found for each size class September 1976, July 1977, and August 1978.

rate. In all censuses a few previously unrecorded larger burrows were found. This is most likely indicative of overlooked burrows in the previous census or, less likely, immigration of spiders which had somehow been evicted from their former burrow into the plot. (Some unrecorded new burrows may have been excavated over smaller burrows thus accounting for some of the extreme jumps in size class, as discussed earlier.) If there is some immigration, there may also be come emigration of spiders not detected by pitfall traps or observation. In any case, however, the number of new, larger burrows was small.

Demographics.—Many species of araneomorphs experience a marked seasonality, with certain size classes restricted to specific times of year. All size classes of *A. riversi*, however, occur simultaneously throughout the year. Remarkably high numbers (538, 635, 596) were present for the three years censused (Fig. 2) in densities as high as ten burrows per 20 cm square. Most of the burrows belonged to sub-adult spiders. (Adult females belonged to size classes 11 and above, the only size classes found with eggs or spiderlings; most adult males emerged from size 10 burrows (Vincent 1980)). The July 1977 frequency of burrows in size classes 4–11, 13 and 14 was similar to the September 1976 population ($\chi^2 = 16.92$, $df = 9$, $P < 0.05$), yet close to half the September 1976 burrows increased or decreased in size, and 99 (18.4%) were missing (Table 1). Size classes 5–11, 13 and 14 in August 1978 were similar in frequency ($\chi^2 = 26.30$, $df = 16$, $P < 0.05$) to the September 1976 and July 1977 censuses (Fig. 2). Notably there were fewer size class 3 burrows than size class 4 burrows and fewer size class 9 burrows than size class 10 burrows in 1976 and 1978 (Fig. 2). The large number of size class 3 and/or 4 spiders relative to the smaller number of spiders in the larger size classes indicates heavy early instar mortality, typical of arthropods, for all three years. The

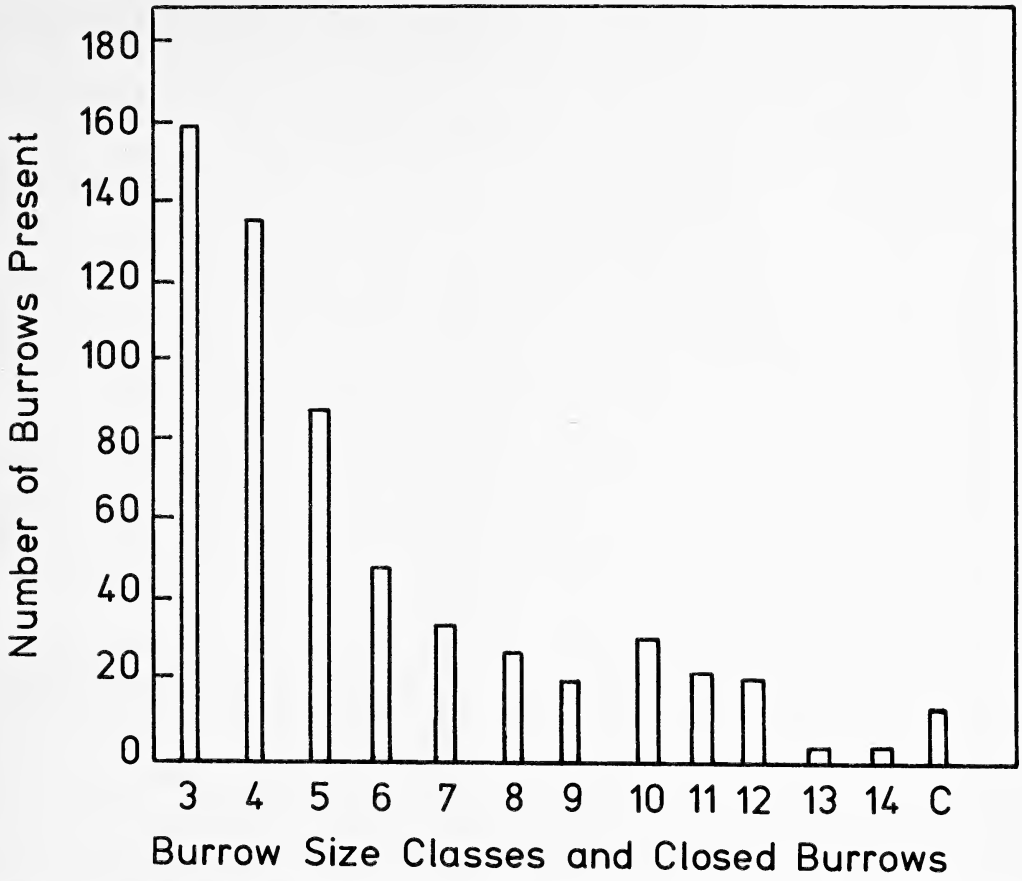

Figure 3.—The number of burrows for each size class occupied by spiders and the number of closed burrows during the May 1978 census.

total numbers of individuals for size classes 3 and 4 varied with time of year, as well as year to year (compare Figs. 2 and 3). However, the large number of new size class 3 and 4 burrows found in April 1977 and May 1978, 205 and 124 respectively, indicate a late fall and/or early spring emergence for spiderlings. This finding is consistent with Coyle's (1971) data. Fewer new burrows of size classes 3 and 4 combined were found July 1977 and August 1978 (40 each) (Vincent 1980).

The drastic decrease in number of size class 3 burrows, the increase in number of size class 4 burrows from May 1978 (Fig. 3) to August 1978 (Fig. 2), and the relatively low number of individuals in size class 3 found in September 1976 (Fig. 2) suggest mortality for size class 3 and/or a transition from size class 3 to a larger size class from the spring to fall. Indeed, of the 187 size class 3 burrows first found April 1977, 59 (31.6%) were missing and 23 (12.3%) grew one size class by July 1977. Of the 87 size class 3 burrows first found May 1978, 10 (11.5%) were missing by August 1978 and 46 (52.9%) grew one size class. The relatively large number of size class 3 burrows found July 1977 compared to August 1978 was a result of the larger number of new size class 3 burrows (187) found April 1977 compared to 87 found May 1978. The number of new spiderlings can be expected to vary extensively, however, as indicated by the range (21–74; $\bar{X} = 46$) in number of eggs produced by nine females adjacent to the study site (Vincent 1980) and a range of 43–80 ($n = 7$) found by Coyle (1971) for a coastal population. Unfortunately, the number and size of clutches within the study site could not be determined. The drop off in numbers of individuals larger than size class 4 (Fig. 2) is due to relatively high mortality (Fig. 4) and growth of size 4 spiders to larger size classes (Tables 1, 2, 3). The more stable distribution of size classes 5 and above appears to have

Table 1.—The total number (n and percent (%) of burrows decreasing, not changing, and increasing in size, and those burrows recorded closed or missing in the July 1977 census of burrows first recorded September 1976. "Change" column reflects current burrow status. Other = old, abandoned, or destroyed.

			Size classes as of September 1976											
Change	n	%	3	4	5	6	7	8	9	10	11	12	13	14
−3	1	0.2				1								
−2	3	0.6				1	1			1				
−1	30	5.6		1	6	6	6	4		2	2	1	1	1
0	160	29.7	8	57	37	18	13	5	5	8	3	4		2
1	137	25.5	29	32	18	18	13	9	8	4	6			
2	56	10.4	3	3	3	10	7	12	8	8	2			
3	15	2.8				1	5	6	2	1				
4	3	0.6		1		1				1				
6	1	0.2		1										
Closed	20	3.7					3	5	1	5	6			
Missing	99	18.4	16	29	16	12	7	4	5	7	1	1	1	
Other	13	2.4	4		4	1	2		1	1				
Total	538		60	124	84	69	57	45	30	38	20	6	2	3

been maintained by a complex combination of spiders growing at different rates over the same time period and varying mortality rates for spiders in each size class (Tables 1, 2, 3).

Growth rates.—Tables 1 and 2 list changes in burrow sizes and conditions over time for the population of burrows censused September 1976 and recensused July 1977 and the population of burrows as of July 1977 and recensused August 1978. Considering all size classes combined (Fig. 5), the 1976 population had a higher proportion of burrows that did not change size (30%), especially size classes 4 and 5 (Table 1), than the 1977 population (12%).

Most burrows increased one or two size classes in the two year period from September 1976 through August 1978; however a few increased as many as five size classes and some decreased as many as four size classes (Table 3).

Feeding studies in the laboratory (Vincent

Table 2.—The total number (n) and percent (%) of burrows decreasing, not changing, and increasing in size, and those burrows recorded closed or missing in the August 1978 census of all occupied burrows as of July 1977; * = other minor changes. "Change" column reflects current burrow status. Other = old, abandoned, or destroyed.

			Size classes as of July 1977											
Change	n	%	3	4	5	6	7	8	9	10	11	12	13	14
−5	2	0.3						1		1				
−3	2	0.3					1	1						
−2	6	1.0			3			1			1			1
−1	24	3.9		4	4	1		1	1	4	4	4	1	
0	74	12.5	4	25	13	7	3	3	2	5	7	2	1	2
1	157	25.6	51	39	20	14	5	2	5	7	7	6	1	
2	67	10.9	7	10	16	8	5	9	2	7		3		
3	27	4.4		3	5	5	5	6	1	2				
4	6	1.0		1	3		1	1						
8	1	0.2	1											
Closed	17	2.8	2		1	2	3	2	2	1	2	1	1	
Missing	203	33.1	74	51	23	12	16	5	9	7	1	5		
Other	28	4.5	2	4	4	5	2		4	3		3	1	
Total	614		141	137	92	54	41	32	26	37	22	24	5	3

Table 3.—The total number (n) and percent (%) of burrows decreasing, not changing, and increasing in size, and those burrows recorded closed or missing in the August 1978 census of all occupied burrows first recorded September 1976; "Change" column reflects current burrow status. Other = old, abandoned, or destroyed.

			Size classes as of September 1976											
Change	n	%	3	4	5	6	7	8	9	10	11	12	13	14
−4	2	0.4					2							
−2	6	1.1			3	3								
−1	13	2.4		3	1	2	3	1		1	1	1		
0	21	3.9	1	5	5	1	2	1		1	2	1		2
1	87	16.2	13	35	12	9	2	4	5	4	2			
2	71	13.2	9	11	16	8	6	6	5	6	3	1		
3	48	8.9	4	8	4	7	8	9	5	2	1			
4	19	3.5		1	2	5	5	5	1					
5	4	0.7		1		1	1	1						
Closed	15	2.8			2	3	4		3	1	1			1
Missing	229	42.6	33	58	37	24	21	15	10	20	8	1	2	
Other	23	4.3		2	2	6	3	3		3	2	2		
Total	538	100.0	60	124	84	69	57	45	30	38	20	6	2	3

1980) revealed that *A. riversi* do molt to smaller or larger sizes depending on food intake. Assuming similar abiotic conditions, the non-uniform growth rate in the field suggests that prey availability or prey capture rates may not always be optimum for some members of this densely packed (up to 635 burrows in a 2.0 × 3.2 m area) population. Perhaps *A. riversi*, like other spiders, molts to a smaller size in the field as a response to starvation to maintain abdominal hydrostatic pressure (Anderson 1974), which is important for locomotion and prey capture (Wilson, 1970).

A non-uniform growth rate may be advantageous to a long-lived species such as *A. riversi* living in dense aggregations. Assuming that maturation of the same clutch is asynchronous, early maturing males would be conducive to outbreeding, especially since adult males appear to die shortly after the mating season (Vincent pers. obs.), whereas adult females live several years in the laboratory and field (presumably with the potential to mate). In this regard, B. Y. Main (pers. comm.) has unpublished data which indicate that males of the long-lived ctenizid *Anidiops* mature a year earlier than females of the same cohort and brood.

Compared to adult females, which continue to molt after maturity (Coyle 1968, 1971), sometimes to larger size class, adult males of *A. riversi* (n = 27) had little variability in sternum (2.00–2.36 mm $\bar{X}$ = 2.16, 1 SD = 0.11) and carapace (3.60–4.16 mm, $\bar{X}$ = 3.92, 1 SD = 0.15) measurements, but a wide range of abdominal sizes (as determined by casual observation) both in the field and laboratory. It may be more advantageous for a small penultimate male to sacrifice some abdominal food reserve, which it could have attained by growing another year, to become sexually active sooner (perhaps for a shorter period of time due to a smaller food reserve), than to delay maturation and suffer more exposure to mortality factors.

Survivorship.—Survivorship of *A. riversi* within this study site varied from year to year and within each size class (Fig. 4). Burrows found September 1976 and recensused July 1977 show a gradual increase in survivorship from size class 3 through size class 8 and for size classes 11 and 14. A similar trend for the ctenizid *Anidiops* has been recorded (B. Y. Main pers. comm.). The drop off in survivors for burrows in size classes 9 and 10 probably reflects both male emergence in search of mates, (see "abandoned" burrows (Vincent 1980)), as well as mortality within the burrow (see "missing" burrows, Tables 1, 2, 3). Size class 10 burrows often contained males or were vacant during and just after the mating season (pers. obs.). Laboratory reared spiders of size 9, 10, and occasionally, 11 often molted to mature males. The emerged males probably die during or shortly after the mating season. Adult males were never found in the field after the mating season (July-September) in this study or in Coyle's (1971). Unfortunately, size classes 12, 13, and

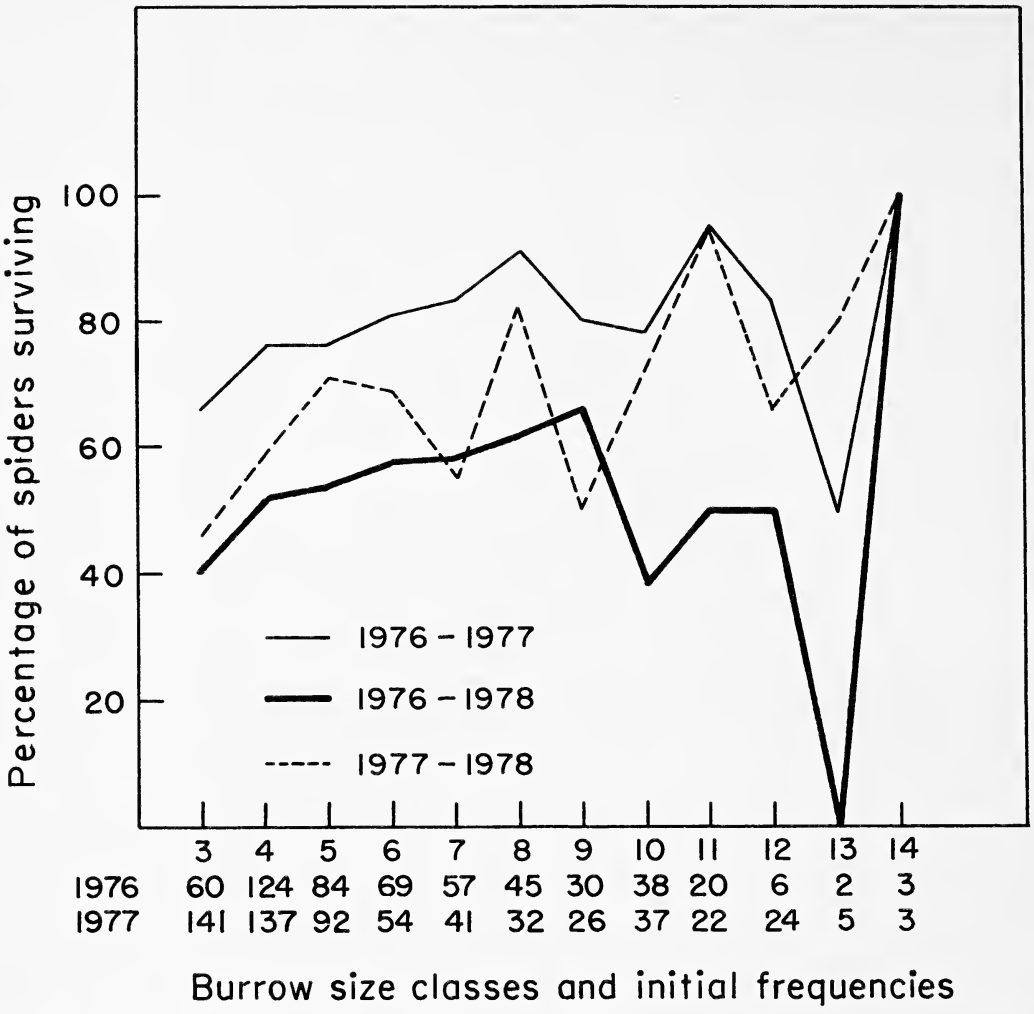

Figure 4.—Survivorship curves, based on burrow censuses, for spiders in initial size classes 3–14 for two one-year periods and one two-year period.

14 had too few members to suggest any trends, yet it should be noted that none of the size class 14 individuals died during this study.

Survivorship was lower for spiders in most size classes, especially size class 3, from July 1977 to August 1978 than from September 1976 to July 1977 (Fig. 4). In the two year interval, 1976–1978, over 50% of the spiders survived for all size classes except 3, 10 and 13. The curve for 1976–1978 resembles the 1976–1977 survivorship curve but is proportionally lower.

Several mortality agents (fungi, nematodes, and acrocerid and tachinid flies) of *A. riversi* were reared in the laboratory from egg sacs or spiders of the larger size classes (Vincent 1983, 1985). Unfortunately, I was unable to rear all the parasites and parasitoids to maturity for complete identification. In most cases the final size class of the dead spider (presumably killed by the action of the agent) was determined. Those mortality agents isolated in the laboratory and the pompilid *Priocnemis oregona* in the field are probably responsible for some of the mortality recorded in the study site. Pathogens or parasitoids were not isolated from spider sizes 3–8 (although one egg sac did contain some dead eggs contaminated with a fungus). This suggests that the more mature spiders are the usual victims of these mortality agents. It is not known at what stage in the spider's development it is first attacked by the agent (except for those parasitized by *P. oregona*).

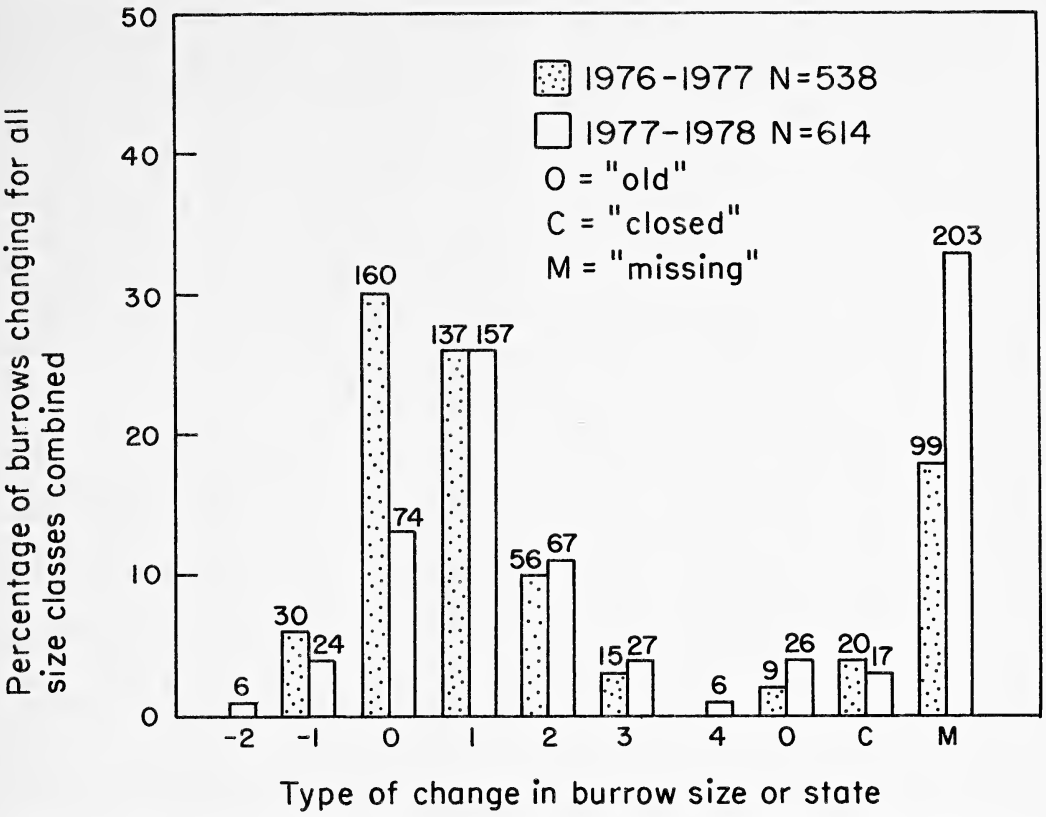

Figure 5.—Change in burrow size or state for all burrows present September 1976 and recensused July 1977 and all burrows present July 1977 and recensused August 1978.

For the present, I suspect desiccation, cannibalism, and starvation to be the most significant mortality factors for spiderlings. On several occasions spiderlings placed in non-moistened containers for transport to the laboratory from the field were found dead and shriveled a few hours later. Larger specimens of *A. riversi* kept under similar conditions did not desiccate. Coyle (1971) also noted that second instar spiderlings, the dispersal stage, desiccated quickly unless kept in high humidity. If desiccation is a factor, it most likely occurs during the dry summer months (see July 1977 and August 1978 demographics for burrows found in the previous spring); there was 1 cm precipitation from June through August both in 1977 and 1978. Cannibalism may be significant, especially in dense populations, since positive geotropism might influence spiderlings dispersing in search of burrow sites to enter occupied spider burrows. The proportionally large number of missing burrows in the smaller size classes during the April 1977 random sample and the May 1978 census suggests that starvation during the winter, when food is limited due to snow cover and cold temperatures, may be a significant mortality factor for spiderlings.

Longevity.—Mygalomorph spiders have been known to live a long time. Baerg (1963) kept certain theraphosids alive for at least 20 years in the laboratory and believed that one specimen lived 26 years (Baerg 1970). B. Y. Main (pers. comm.) estimates that a ctenized, *Anidiops villosus* (Rainbow), can live at least 23 years in the field. In estimating longevity of *A. riversi*, it is necessary to approximate several factors: date of oviposition and eclosion, date of emergence and burrow establishment, number of years to reach a size 14 (the largest size class), and the tenure of this size class. Since oviposition and eclosion occur in the summer and early fall respectively, and emergence in the following spring, the spiders in the size 3 burrows in September were about a year old. Based on extrapolations from the growth rates observed for all size classes from September 1976 to August 1978 (Table 3), the time it could take a size 3 burrow to become a

size 14 varied considerably. Size classes 3 and 4 most frequently grew one size class in two years, size class five most frequently grew two size classes in two years, size class seven commonly grew three size classes in two years, and sizes classes 10 and 12 could grow two size classes in two years. Using these growth rates as an estimate, it would take some burrows 13 years to reach size 14. Other extrapolations, from Table 3, could reasonably be used to estimate minimum to maximum time to size class 14. Finally, in September of 1976 there were three size 14 spiders; on 22 September 1979, three years later, one was still alive. I estimate, therefore, that under similar environmental conditions and growth rates *A. riversi* can live in the field at least 16 years.

Most spiders (araneomorphs) live one to three years depending on the species (Bonnet 1935). Why do mygalomorphs live so long? Main (1976), referring to arid adapted trapdoor spiders, suggests it is advantageous for an adult female to be able to wait out several continuous years of unfavorable weather conditions that may disrupt the emergence of reproductively active males. In the fall, at Blodgett Forest, few females with eggs or brood were collected, yet during the spring many gravid females were collected. Lack of egg deposition could be due to insufficient acquisition of food during the summer for complete egg development by fall. Living several years would increase the chances of obtaining enough food. Unlike some araneomorphs (Turnbull 1964, Riechert 1976), *A. riversi* does not appear to change initial burrow locations to take advantage of potentially more productive areas.

In addition to biotic mechanisms, *A. riversi* may achieve a relatively long life because of its sheltered microhabitat. It has been suggested that the burrowing desert scorpion *Paruroctonus mesaensis* (Vaejovidae) achieved its long life (ca. five years) as one result of its stable and predictable subterranean microhabitat (Polis & Farley 1980). The burrows of *A. riversi* protect them from wind, to some extent rain and runoff, and some potential predators. Additionally, an influx of moisture from surrounding soil (Vogel 1978) and regulating the turret entrance opening (Vincent pers. obs.) may help prevent desiccation during the dry California summers.

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ASPECTOS DE LA BIOLOGÍA REPRODUCTIVA DE *LINOTHELE MEGATHELOIDES* (ARANEAE: DIPLURIDAE)

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ABSTRACT. Of 50 specimens of *Linothele megatheloides* (Raven) growing under laboratory conditions, only 22 reached a sexually mature state after 10 and 11 ecdyses. The average number of eggs per sac was 161.5; the average egg diameter was 22 mm. The spiders were monitored in the laboratory to determine the inter-instar rate of growth. Eggs held in paraffin and carboxymethyl-cellulose developed only to gastrula. Under laboratory conditions, spiders did not build complete egg sacs, and the eggs were eaten. Several egg sacs were destroyed by fungus and parasitoids. The time of emergence of the spiderlings after oviposition was between 23 and 27 days. The reproduction period occurred between April and October and was apparently related to rain and relative humidity. The spiders have little parental care of the eggs and spiderlings.

RESUMEN. De los 50 ejemplares de *Linothele megatheloides* (Raven), creciendo bajo condiciones de laboratorio, solamente 22 llegaron a la madurez sexual, luego de entre 10 y 11 mudas. Las arañas se monitoriaron en el laboratorio para determinar el incremento entre un instar y el próximo. Los huevos incluídos en parafina líquida y en carboximetil celulosa, solamente llegaron a gástrula. Bajo condiciones de laboratorio, las arañas no construyeron la ooteca completa y sus huevos eran normalmente comidos por ella. Varios sacos de huevos fueron parasitados y destruidos por hongos y parasitoides. El tiempo de emergencia de las arañitas luego de ser puesta la ooteca estuvo entre 23 y 27 días. El período de reproducción estuvo entre abril y octubre, situación aparentemente relacionada con el incremento en humedad relativa. Las arañitas no mostraron inversión parental alta con sus huevos y crías.

En concordancia con los resultados obtenidos por Paz (1988), al estudiar por primera vez en el neotrópico aspectos de la biología de *L. megatheloides* en bosques primarios de Panamá y Colombia relacionado con algunos patrones de su conducta, se consideró que otras situaciones deberían ser investigadas y de manera especial su biología reproductiva. Así, se diseñó esta segunda fase con los objetivos siguientes: verificar si las arañas se reproducen a través de todo el año, y si existe alguna relación con las condiciones climáticas reinantes en el área de estudio; determinar el tiempo promedio de incubación; establecer la posible relación entre el tamaño de la caparazón y algunos apéndices (tarso uno; largo quelícero y palpo) con la madurez sexual; el peso y tamaño de la ooteca y el número promedio de huevos por ooteca, número posible de mudas necesarias para alcanzar su madurez sexual; tiempo y mecanismo de dispersión de las arañitas y hasta donde fuese posible seguir los primeros estadios embrionarios dentro del huevo y la conducta maternal de la araña frente a su ooteca y arañitas.

MÉTODOS

El área de estudio correspondió a la misma descrita por Paz (1988). Allí se seleccionaron algunos nidos al azar, se marcaron con tiras de telas de color, con el objeto de hacer más fácil su posterior localización, especialmente en horas nocturnas.

En el área se capturaron 50 arañas al azar desde púber hasta adultas, según método descrito por Paz (1988). A las mismas se les midió largo y ancho de la caparazón; largo del palpo, quelícero (no incluída la uña) y del tarso uno, con el fin de establecer posibles correlaciones de su crecimiento y la madurez sexual. A las arañas normalmente se les regresaba a su nido luego de medirlas o bien se seleccionaban algunas con abdomen muy redondeado (consideradas grávidas) para traerlas al laboratorio en donde se les colocaban en cajas separadas de plexiglas.

También en caso de encontrar nidos con arañas grávidas o con ootecas, se les marcaba para hacerles futuros seguimientos, o se colectaban sus ootecas las que traídas al laboratorio se les

medía su diámetro, se pesaban en una balanza digital Quantum-Q-800, se abrían para contar sus huevos, medirles su diámetro e incluírlos en un recipiente de plástico de 24 depresiones de 1 cm; 12 de los cuales contenían CMC y 12 con parafina líquida, para observar posibles cambios embrionarios. Otras ootecas, se colocaban directamente en cajas de petri con algodón en una incubadora de ICOPOR, con una fuente térmica de 60 W, temperatura entre 26–28 °C y humedad relativa entre 80–90%.

Con las ootecas producidas en el laboratorio, se trabajó en igual forma y sirvieron para determinar el tiempo de permanencia de las crias dentro de ellas, desde la oviposición, hasta su eclosión.

Arañitas inmaduras de pocos días de haber salido de la ooteca pero aún asociadas con ella, fueron coleccionadas, lo mismo que algunas que ya la habían abandonado. A las primeras se les colocaba en pequeños recipientes plásticos dentro de la incubadora, para hacerles seguimiento post-embrionario de muda y de interacción entre ellas, para completar las observaciones de las nacidas en el laboratorio. El seguimiento de muda y de correlación de las estructuras somáticas a través del crecimiento, se inició con ejemplares de segundo instar, correspondiente a aquellas arañitas recién salidas de su ooteca al romperla. Se tomaban de 6–8 ejemplares por cohors, se pesaban cada una y luego se mataban en alcohol al 20% para medirles las estructuras mencionadas.

A partir de este estadio, las sucesivas mediciones se hicieron sobre las respectivas exuvias cada vez que mudaban y se pesaban 2 ó 3 días después de mudar. La pesada se hizo en una balanza analítica hasta el instar 8, y a partir de este estadio, en la digital Quantum en pequeños recipientes de plástico. Los valores obtenidos para ocho ejemplares de tres camadas diferentes para cada instar se registraban y se determinaba el tiempo entre una muda y la siguiente.

A las arañitas se les alimentó cada dos días inicialmente con *Drosophila melanogaster* y otras especies de las cepas existentes en el laboratorio de genética y a partir del segundo instar con moscas domésticas y pequeños homópteros, coleópteros, ortópteros, hemípteros e isópodos, cuyos tamaños se incrementaban en concordancia con los instar. A medida que las arañitas crecian se separanan en grupos menores para evitar predación entre ellas.

Con las adultas se hicieron observaciones, de fase precopulatoria, copulatoria y post-copulatoria. Para la nominación de los instares se siguio la nomenclatura de Vachon (Foelix 1982).

Tabla 1.—Valores promedios mensuales y anuales de la humedad relativa (HR) con sus promedios, máximos y mínimos, precipitación y el número de días que llovió por mes en el área de estudio. Tomado del "Calendario" Meteorológico del Himat, (Inst. Hidrológico, Meteorologíco y adecuación de tierras) para Colombia 1988.

Mes	HR %	°C ($\bar{x}$)	°C ($\bar{x}$) maximo	°C ($\bar{x}$) minimo	Precip. (mm)	Días de lluvia/ M
Enero	88	26	30	23	561	23
Febrero	86	26	30	23	480	20
Marzo	87	27	31	23	513	21
Abril	87	27	31	24	569	23
Mayo	87	27	31	23	705	26
Junio	87	27	32	23	760	24
Julio	86	27	31	23	784	26
Agosto	86	26	31	23	899	27
Septiembre	87	26	31	23	700	25
Octubre	88	26	31	23	611	26
Noviembre	87	26	30	23	692	25
Diciembre	88	26	30	23	667	25
$\bar{x}$ anual	87	26	31	23.1	661.7	24.25

Los cambios meterológicos a través del año con los registros promedios de humedad relativa, temperatura y aquellas precipitación pluvial mensual se obtuvieron del boletín mensual de la estación del HIMAT para esta área del Chocó (1988). Desde febrero 1988 hasta julio 1989 se visitó cada mes y medio el área de estudio, con un período de permanencia entre ocho y cinco días.

RESULTADOS Y DISCUSION

De los valores de factores ambientales la precipitación suele incrementar manifiestamente a partir del mes de abril hasta septiembre, alcanzando su máximo durante el mes de agosto. Existe aparentemente una relación entre la época en que se reproducen estas arañas y el incremento de los períodos de humedad ambiental. Sólo a partir de los últimos días del mes de abril del primer semestre del 1988 y 1989, al incrementar las lluvias, se encontraron las primeras ootecas sin reventar (tres en el 1988 y dos en el 1989).

Caparazón, ooteca y número de huevos.—El número de huevos promedio de siete ootecas abiertas al azar fue de 161.5 (cuatro procedentes

Tabla 2.—Aquí se representan las ootecas, con sus correspondientes valores para ancho, largo, peso de cada una y su número correspondiente de huevos. Los asteriscos representan las ootecas abiertas para contar su contenido.

N° ooteca	Ancho caparazón (cm)	Largo ooteca (cm)	Peso ooteca (g)	N° de huevos
1	.8	2.4	1.5	No abiertos (incubación)
2	.9	2.1	No fué reiterada (oofagia)	—
3	.9	2.8	1.7	97
4	1.0	2.9	1.8	132
5	1.2	3.0	1.7	No abiertos (incubación)
6	1.2	3.0	No fué reiterada (oofagia)	—
7	1.2	2.9	1.6	184
8	1.1	2.8	No fué reiterada (oofagia)	—
9	1.1	2.8	No fué reiterada (oofagia)	—
*10	1.1	2.9	1.9	209
*11	1.0	2.1	1.9	183
12	.9	2.1	No fué reiterada (oofagia)	—
*13	1.3	2.8	1.9	207
*14	1.3	2.9	2.0	219
15	1.3	2.6	3.0	No abiertos (incubación)
16	1.3	2.8	2.0	No abiertos (incubación)

del campo y tres del laboratorio), no se abrieron para evitar alta pérdida de arañitas. El número de éstos por saco tendió a incrementar con los mayores valores del ancho de la caparazón, largo y peso de la ooteca, tabla 2. El diámetro promedio de los mismos para 100 tomados al azar de cinco sacos (5 × 20) fué de 2.2 mm (rango de 1.72–2.45).

Miyashita (1987) informa que Valerio (1976), al trabajar con *Achaearanea tepidariorum* (Koch) en Centro América (Costa Rica) encontró que el potencial promedio de huevos puestos por una hembra al año es de 3211.9 y 14.1 ootecas, posiblemente debido a una mayor presión de selección de predación. Peaslee (1983) reportó para *Octonoba octonarius* (Muna), un número promedio de huevos por ootecas de 78 (rango 45–107). Galiano (1972, 1973) estudiando el desarrollo post-embrionario de arañas de Theraphosidae y Dipluridae en la Argentina, encuentra para *Acanthoscurria sternalis* (Pocock) un promedio de huevos de 1 050–1 130 con diámetros de 1.3–1.6 mm, para *Avicularia avicularia* (Linnaeus) de 70–112 huevos con diámetros de 3.86–4.06 mm, y para *Ischonothele siemensi* (Cambridge) de 80–150 huevos con diámetro de los 0.9–1 mm.

En cinco sacos (2, 6, 8, 9 y 10) puestos bajo condiciones de laboratorio no retirados del recipiente con la araña, fueron consumidos por ésta. Estos casos de oofagia estarían relacionados con factores adversos que bajo condiciones de laboratorio, inducirían a no colocar las tres capas de seda con las que suelen proteger y aislar sus huevos, facilitando su consumo luego de ovipositardos.

Oviposición vs. incubación: Arañas grávidas tejen en un área de su red una especie de tela cuyo tejido es mucho más fino y fusionado que el resto de ella, semejando una verdadera "manta", de color blanco, en parte similar a la que construye cuando va a mudar. Allí, la araña deposita primero un líquido claro bastante gelatinoso, e inicia la deposición de sus huevos alternadamente, y luego comienza el tejido de las capas de seda para aislar la ooteca a manera de cámara (Fig. 1). Bajo condiciones de cautiverio, la colocación de la última capa, no se observo, quedando así los huevos expuestos. Esta capa poco elástica y altamente resistente, además de aislar y proteger los huevos, servirá por su puesto para mantener la humedad en el interior del saco, proveída por el líquido siruposo. El número de ootecas por epoca de reproducción fue de una en condiciones de laboratorio.

El tiempo de permanencia dentro del saco, se estimó con tres ootecas (1, 5, y 16) las cuales no se abrieron. La uno procedía del campo con fecha de oviposición junio 4, 1988 y las dos restantes del laboratorio puestas en julio 26, 1988, agosto

Figura 1.—*Linothele megatheloides*, al finalizar una oviposición. Obsérvese la tupida red del saco y su abdomen muy contraído.

6, 1988. La emergencia de las arañitas fue en su orden a los 22, 27, y 23 días, por lo cual el tiempo promedio de permanencia se estimo en 24.5 días, con rangos de 22–27.

El verdadero tiempo de incubación (período entre la oviposición y la prelarva intracoriónica), no fue determinado, ya que los huevos transferidos a CMC y parafina líquida no alcanzaron a pasar de la fase de gástrula (la que se caracterizó en ambos medios por el recogimiento de blastodermo alcanzado entre las 48–72 h).

Durante el desarrollo embrionario, observó que buen nṁero de huevos se ennegrecen o endurecen prontamente, lo que se puede atribuir a que no estaban fecundados o haber sido parasitados (Fig. 2).

De las ootecas abiertas, no fue posible determinar con seguridad el nṁero de huevos fecundados, ya que al ser la oviposición secuenciada es normal esperar diferencias en el desarrollo embrionario y post-embrionario entre los huevos fecundados, lo que se refleja en las arañitas al emerger del saco.

Galiano (1972) encontró que la dipluridae *Ischnothele siemensi* (Cambridge) tiene un período de incubación de los 10–12 días en Argentina; Eason (1969), reporta que el período para *Pardosa lapidicina* (Emerton), es de 23.4 días con rangos de 17–30, dependiendo de las condiciones ambientales; para *Cyrtophora moluccensis* (Doleschall), el tiempo estimado por Berry (1987) fue de 24.4 días con rangos de 24–28; Moore (1977) reporta para *Nephila clavipes* (Linnaeus) un período aproximado de un mes para el sur de Norte América, siendo menor a nivel trópical, posiblemente por las condiciones ambientales más favorables.

Estas arañas, de acuerdo a lo observado en el campo y laboratorio, no suelen cuidar sus ootecas, lo que fue normal encontrar en algunas especies de Lycosidae, Pisauridae, Sparassidae (Heteropodidae), Clubionidae, Araneidae, Theridiidae y otras familias que permanecían vigilantes frente a ellos.

Emergencia desde la ooteca y dispersión: Las arañitas al emerger del saco, no suelen abandonarlo, sino que permanecen sobre él, en una pequeña red comunal. Allí permanecen hasta la segunda muda (I–2) y a partir de éste instar, comienzan a tratar de construir pequeñas redes individuales cada vez más separadas, hasta alcanzar su tercer instar. En este estadio comienzan a perseguirse y mantener una mayor distancia individual, conducta de agresión que se incrementa

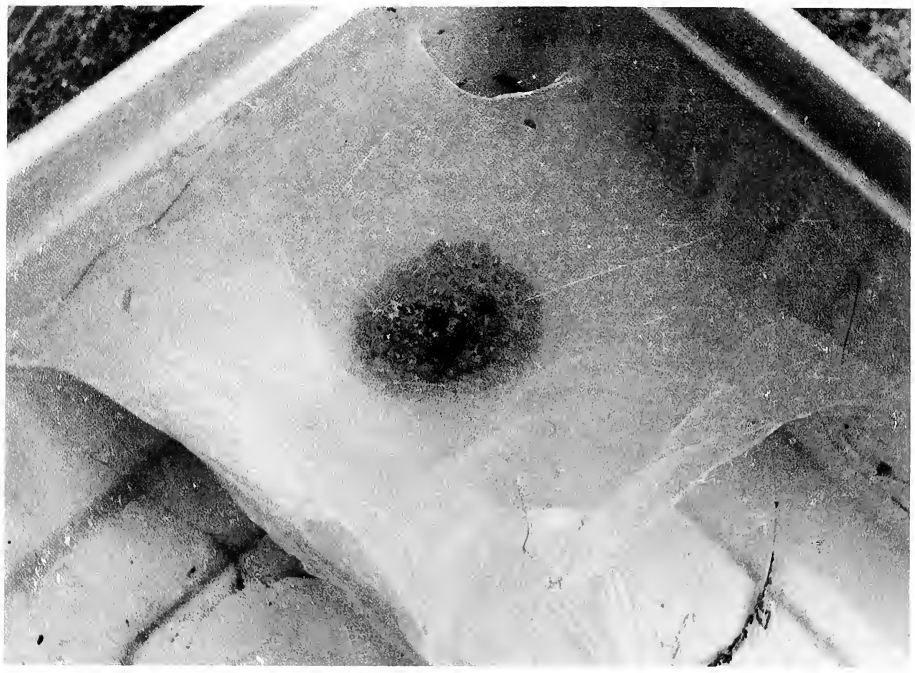


Figura 2.—Ooteca puesta en cauterio, con sus huevos no protegidos. Algunos han comenzado a ennegrecerse y corresponden normalmente a no fecundados o haber sido parasitados.

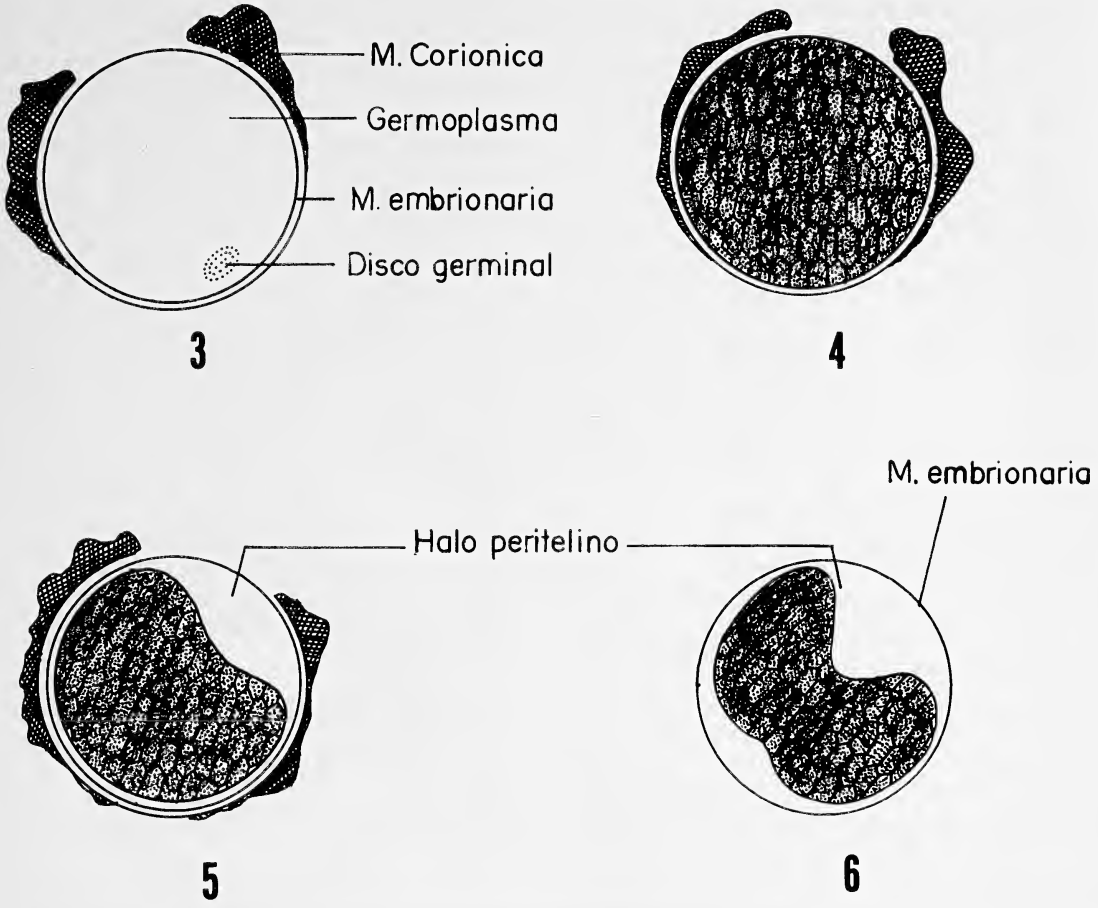
con los sucesivos estadios. Fue necesario en este estadio separarlas en grupos más pequeños y en recipientes de mayor espacio, para evitar el canibalismo. Por esta razón, a partir del quinto instar, cada recipiente sólo contenía dos ejemplares I–7. En el campo, es bastante posible que a partir del I–3 es cuando las arañitas comienzan a dispersarse cada vez más.

Relación sexual.—Fue notorio el desfase observado entre hembras y machos, en los ambientes naturales y en cautiverio. Es así que durante los seis meses de trabajo en el Parque de la Soberanía de Panamá, sólo encontraron dos machos sexualmente maduros y en casi dos años de salidas de campo al área del Chocó, cinco. De las arañas levantadas en condiciones de laboratorio, hasta su madurez sexual ($n = 19$), sólo una emergida de una ooteca colocada en mayo 1988, luego de la 1O° muda, el extremo distal de sus palpos evidenció transformación en gonopidos. Esta diferencia en la relación de sexos se podría explicar sobre el hecho que al llegar a su madurez sexual (entre la 9–10 mudas), los machos abandonan sus redes (más pequeñas) e inician la fase deambulatoria en busca de hembras receptivas para copular, con lo cual se expondrían más a los depredadores.

Desarrollo embrionario y post-embrionario.—Con los huevos colocados en parafina líquida, para seguir su desarrollo embrionario de acuerdo al método de Holm/Galiano (1972, 1973a, 1973b) y los incluídos en CMC, con igual objeto, no fue posible hacer este seguimiento. A pesar que la membrana coriónica era lisada y la germinal o embrionaria permanecía normal, el desarrollo del embrión sólo alcanzó a llegar a "gástrula". Su detención en CMC, posiblemente se debe a que esta sustancia se endurece poco a poco y a las 72 h, estaba prácticamente semisolificado. En la parafina a pesar que ésta permaneció normal, los estadios tampoco continuaron, ignorándose su causa.

Entre las 8–2 horas después dela oviposición, se podía observar al microscopio y al stereo, las primeras etapas de división del disco germinal blanquesino, y a las 24 h, éste ya había dado origen al blastodermo, con aparatentes células poligonales (Fig. 3–6).

La "prelarva", se obtuvo de ootecas abiertas, cuyos huevos contenían la arañita protegida por la cutícula embrionaria transparente, sobre la cual no fue fácil detectar el área donde estarían los dientes de eclosión y responsables de la ruptura de la membrana del corión. Esta etapa se carac-



Figuras 3–6.—Primeras etapas del desarrollo embrionario de huevos de *L. megatheloides*. 3, huevo con corión reventado y el germoplasma con su disco germinal dentro de la membrana; 4, capa de blastodermo con sus células poligonales; 5, 6, contracción del blastodermo y exposición del espacio perivitelino.

teriza porque el cefalotórax está manifiestamente inclinado hacia abajo, las patas plegadas sobre los flancos pleurales, las espinneretas posteriores son más desarrolladas que las anteriores y no hay cerdas, ni tricobotrias ni pigmentación somática (Fig. 7, 8).

La "larva" (deutovium), equivale al primer instar postembrionario (I–1). Aqui la pre-larva se ha liberado de la membrana embrionaria o cuticula (primera exuvia), al mudar por primera vez; sus miembros y cuerpos presentan cerdillas, se evidencia podomerización pero no tricobotria en sus patas, las que aparecen no plegados al abdomen; queliceros separados, uñas visibles, pigmentación foliar y mancha ocular sólo ligeramente perceptibles. Esta fase es dentro de la ooteca.

El tercer estadio (I–2) post-embrionario corresponde a la "ninfa", en donde los procesos dentarios de las uñas tarsales y quelíceros son bien detectables, lo mismo que los ojos, el patrón de pigmentación del folium y cefalotórax, espinnereta posterior muy elongada, placas epigástricas y cerdas de sus miembros y cuerpo visibles. En este estado salen de la ooteca y son excelentes constructoras de redes adyacentes al saco (Fig. 9).

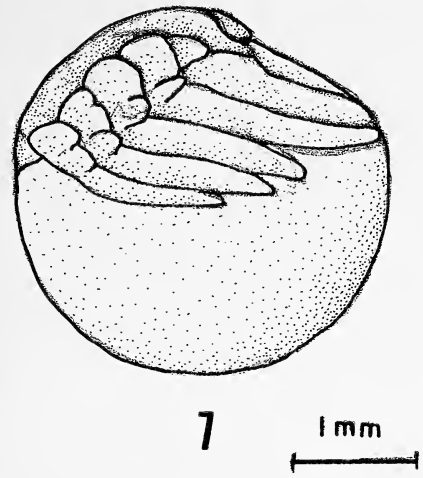
El tiempo entre el I–1 y el I–2 estuvo de los 20–26 dias, para $n = 19$ ejemplares. A partir del I–1, se procedió a determinar el *posible factor de progresión de crecimiento* (FPC) relacionado con el incremento promedio en el tamaño de algunas de sus partes y peso entre un instar y el próximo. Los valores promedios tomados de las mediciones directas de cada estructura utilizada y del peso somático, su respectivo estadio y FPC, se representan en las tablas 3 y 4, lo mismo que el tiempo entre una muda y la siguiente. Nótese

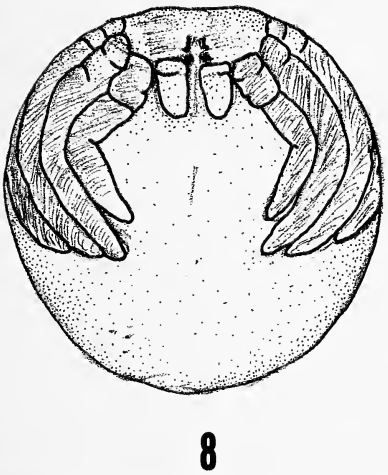
Tabla 3.—Relación de valores promedio de las variables utilizadas y sus respectivos estadios post-embrionarios de *Linothele megotheloides,* luego de emerger de su ooteca y alcanzar su madurez sexual. n = 22; PS = Peso somatico; LQ = Largo quelíceros; LP = Largo palpal; AC = Ancho caparazón (cm); T_1 = Largo tarso uno (cm); $\bar{x}$FPC = FPC de las medias; I = Instar; DTFPC = Desviación típica del FPC; FPC = Factor de progresión de crecimiento; T = Tiempo promedio intermuda en días.

Instar	PS (g)	FPC	AC	FPC	T_1	FPC	LP	FPC	LQ	FPC	Tiempo
Muda-2	0.02		0.19		0.14		0.31		0.08		
I-1		2.23		1.28		1.44		1.99		1.23	23
Muda-3	0.05		0.23		0.20		0.61		0.11		
I-3		1.38		1.07		1.12		1.16		1.33	29
Muda-4	0.07		0.23		0.23		0.71		0.14		
I-4		2.27		1.23		1.17		1.30		1.36	35
Muda-5	0.15		0.31		0.27		0.92		0.19		
I-5		2.48		1.26		1.15		1.23		1.19	42
Muda-6	0.38		0.39		0.31		1.14		0.23		
I-6		1.76		1.24		1.29		1.25		1.22	47
Muda-7	0.67		0.48		0.39		1.42		0.28		
I-7		1.86		1.22		1.17		1.17		1.16	49
Muda-8	1.25		0.58		0.46		1.66		0.32		
I-8		1.79		1.34		1.27		1.23		1.20	72
Muda-9	2.23		0.78		0.59		2.04		0.39		
I-9		1.28		1.37		1.28		1.15		1.12	91
Muda-10	2.86		1.08		0.76		2.35		0.43		
I-10		1.24		1.19		1.37		1.46		1.26	109
Muda-11	3.56		1.28		1.04		3.43		0.54		
$\bar{x}$FPC		1.81		1.25		1.25		1.33		1.24	
DTFPC		0.44		0.10		0.08		0.12		0.17	

Tabla 4.—Valores de la $\bar{x}$, su DT y el respectivo factor de progresión de crecimiento (FPC) para cada uno de los instares obtenido en condiciones de laboratorio hasta llegar a su madurez sexual. n = 22; PS = Peso somático; AC = Ancho caparazón; LP = Largo palpal; T_1 = Largo tarsal uno; LQ = Largo quelícero.

Instar		PS	AC	LP	T_1	LQ
	$\bar{x}$	0.02 ± 0.0	0.2 ± 0.0	0.3 ± 0.0	0.1 ± 0.0	0.1 ± 0.0
I-2	FPC	1.0 ± 0.1	1.0 ± 0.1	0.9 ± 0.1	1.0 ± 0.2	0.9 ± 0.1
	$\bar{x}$	0.1 ± 0.0	0.2 ± 0.0	0.6 ± 0.1	0.2 ± 0.0	0.1 ± 0.1
I-3	FPC	1.4 ± 0.1	1.1 ± 0.1	1.1 ± 0.3	1.1 ± 0.3	1.0 ± 0.5
	$\bar{x}$	0.1 ± 0.0	0.3 ± 0.0	0.7 ± 0.0	0.2 ± 0.0	0.1 ± 0.0
I-4	FPC	1.1 ± 0.0	1.1 ± 0.2	1.0 ± 0.2	1.0 ± 0.13	1.1 ± 0.4
	$\bar{x}$	0.2 ± 0.2	0.3 ± 0.0	0.9 ± 0.0	0.3 ± 0.0	0.2 ± 0.0
I-5	FPC	0.7 ± 0.2	0.9 ± 0.2	1.0 ± 0.0	1.0 ± 0.2	0.9 ± 0.1
	$\bar{x}$	0.4 ± 0.2	0.4 ± 0.1	1.1 ± 0.1	0.3 ± 0.0	0.2 ± 0.0
I-6	FPC	1.6 ± 0.7	1.2 ± 0.2	1.0 ± 0.2	1.0 ± 0.1	1.1 ± 0.2
	$\bar{x}$	0.7 ± 0.2	0.5 ± 0.0	1.4 ± 0.1	0.4 ± 0.1	0.3 ± 0.0
I-7	FPC	0.7 ± 0.0	0.9 ± 0.0	1.0 ± 0.1	1.0 ± 0.1	0.9 ± 0.1
	$\bar{x}$	1.3 ± 0.1	0.6 ± 0.0	1.7 ± 0.0	0.5 ± 0.0	0.3 ± 0.0
I-8	FPC	1.1 ± 0.2	1.0 ± 0.0	1.0 ± 0.1	1.0 ± 0.1	1.0 ± 0.1
	$\bar{x}$	2.2 ± 0.1	0.8 ± 0.0	2.0 ± 0.0	0.6 ± 0.1	0.4 ± 0.0
I-9	FPC	0.7 ± 0.5	0.8 ± 0.3	1.0 ± 0.0	1.0 ± 0.0	0.9 ± 0.0
	$\bar{x}$	2.9 ± 0.2	1.1 ± 0.1	2.3 ± 0.0	0.8 ± 0.1	0.4 ± 0.1
I-10	FPC	0.9 ± 0.1	1.1 ± 0.1	1.1 ± 0.4	1.0 ± 0.1	1.1 ± 0.2





Figuras 7, 8.—Estadio de la "pre-larva" dentro de la membrana embrionaria. 7, vista lateral; 8, vista frontal.

que el valor del FPC suele normalmente decrecer en concordancia con el incremento en muda al irse alcanzando la madurez sexual. Estos valores asi obtenidos, se utilizaron con la formula del método teórico de correlación de crecimiento de Franke & Sisson (1984).

Cuatro arañas que ovipositaron en cautiverio, mudaron entre los 45–57 días después evidenciando que siguen mudando luego de llegar a su madurez sexual. A las 50 arañitas tomadas al azar en el campo desde joven hasta adultas se les determinó los valores correspondientes al tarso uno (T_1), largo palpo (LP); largo quelícero (LQ); ancho caparazón (AC) y largo caparazon (LC), para establecer su posible correlación. Encontrándose que el mayor valor correspondió al valor entre el ancho y el largo de caparazón (r = 0.935) y el menor a la relación entre el largo del quelícero y el tarso uno (r = 0.065). Los valores máximos, mínimos, su media, *d.t.* y limites de confianza de las medidas se dán en la tabla 5.

Tabla 5.—Valores en cm de las variables anatómicas para n = 50 y un nivel de confidencia del 95% (0.05). $LC_{\bar{x}}$ = Limites de confianza de la $\bar{x}$.

	Máximo	Mínimo	$\bar{x}$	DT	$LC_{\bar{x}}$
LC	1.5	0.5	1.1	0.3	1.2 1.0
AC	1.3	0.4	1.0	0.2	1.0 1.0
T_1	1.0	0.3	0.7	0.2	1.0 0.9
LQ	0.9	0.3	0.6	0.1	0.6 0.5
LP	3.6	1.0	3.0	0.6	3.0 2.7

Stratton & Lowrie (1984) encuentran que estas relaciones son más positivas en hembras que en machos de *Schizocosa mccooki* (Montgomery); Austin (1984) reporta que el valor de la correlación entre tamaño de la caparazón y el número de huevos para *Clubiona robusta* (Koch) fue de r = 0.81 y el número de mudas requeridas para la madurez sexual de 9–10 a para hembras y 7–9 para machos.

Baerg (1928) encontró que machos de *Eurypelma californica* (Ausserer) (tarántula), llegaron a su madurez sexual leugo de 10–11 años, con un número de mudas de 22 y una longitud cefalotoráxica de 47.3 mm y que eran poco abundantes.

Parasitismo.—Se encontraron ácaros asociados externamente con las ootecas, las que al parecer no se comportan como verdaderos parásitos, al no ver ninguno de ellos romperla o devorar sus huevos. Cuatro ootecas tomadas en el campo, presentaban huevos posiblemente de Hymenoptera o Diptera. Tres arañas se encontraron en el campo dentro de la cueva, muertas y cubiertas de un hongo filamentoso. Igual cosa sucedió con dos en cuativerio. El hongo correspondió a un deuteromicete, de acuerdo a su patrón de crecimiento.

Algunos investigadores han reportado que buen número de muertes de arañas son debidas a varias fuentes de parásitos o parasitoides, tal es el caso de Poinar & Thomas (1985), McQueen (1978), Raymond (1984), y Nentwig (1985).

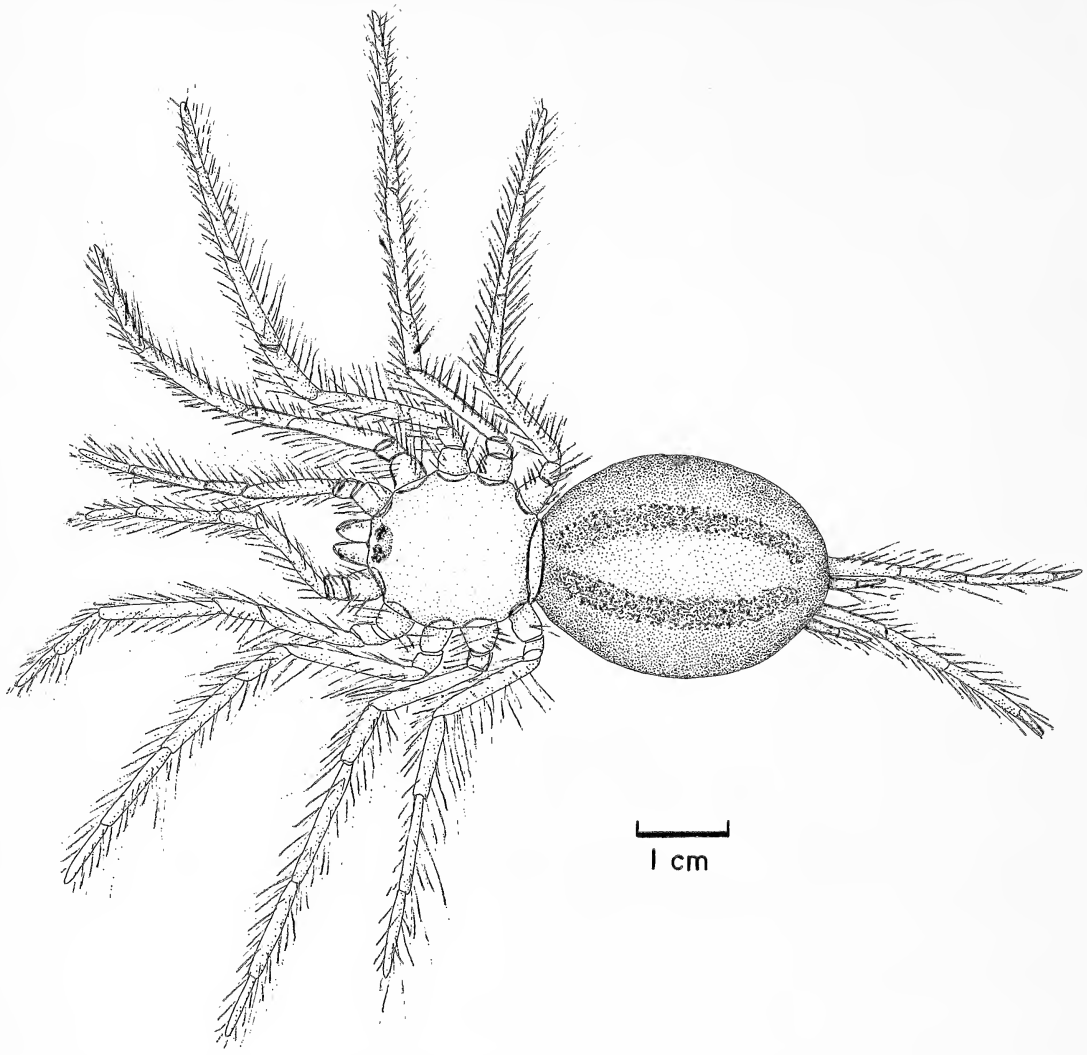


Figura 9.—Tercer estadio post-embrionario (ninfa), correspondiente al segundo instar (I–2), luego de emerger de la ooteca.

Conducta pre-copulatoria.—Una hembra que había ovipositado en julio, se le agregó un macho capturado en el campo en septiembre 1988 el que carecía de espermatóforos en sus gonopodios. Al hacer contacto con la hembra, la tocó sigilosamente con los extremos de sus patas delanteras, ante lo cual ésta se retiraba varios centímetros; esta conducta se repitió por tres ocasiones, pero en la cuarta la hembra reaccionó persiguiéndolo hasta una distancia de unos 12 cm. En el sexto encuentro ambos se enfrentan inicialmente tocándose con los extremos del tarso. Esta actitud al parecer de reconocimiento, se repitió con un acercamiento mayor entre las parejas, sin que la hembra tratara de perseguir o lesionar al macho. El enfrentamiento fue de duración variable en cuanto a tiempo desde 2.5 hasta los 13 min. El macho en ocasiones trató de tocar el área ventral de la hembra con sus palpos, sin obtener reacciones negativas por parte de ésta. Las observaciones de esta actividad precopulatoria fueron realizadas en tres ocasiones con períodos de dos horas. Hembras receptivas al introducirle el macho no mostraron conducta agonística, lo que si se evidenció con hembras grávidas (no receptivas).

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SURVIVABILITY OF OVERWINTERING *ARGIOPE AURANTIA* (ARANEIDAE) EGG CASES, WITH AN ANNOTATED LIST OF ASSOCIATED ARTHROPODS

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ABSTRACT. Overwintering egg cases of the black and yellow garden spider, *Argiope aurantia* Lucas (Araneae: Araneidae), were observed during the late winter and early spring of 1985, 1986, and 1987 in Washington County, Mississippi. Of 120 egg cases monitored in the field in 1985, only three remained undamaged by the period of peak spiderling emergence in May. An additional 115 field-collected egg cases were observed in the laboratory in 1985. A total of 23,840 *A. aurantia* spiderlings emerged from the lab egg cases (mean = 341), with 1212 spiderlings emerging from one undamaged egg case. Adults or pupae of either the parasitic ichneumonid wasp, *Tromatopia rufopectus* (Cr.), or the parasitic chloropid fly, *Pseudogaurax signatus* (Loew), emerged from 56% of the field-collected egg cases. Nineteen species of insects, representing 19 genera, 15 families and 5 orders were collected from lab-reared egg cases in 1985. In addition, 11 species of spiders were recovered from *A. aurantia* egg cases. In 1985, 97% of the egg cases observed in the field showed evidence of bird damage. In both 1986 and 1987, 100% of the egg cases were damaged by birds.

The black and yellow garden spider, *Argiope aurantia* Lucas, is a common orb-weaving spider found throughout the eastern part of the United States and along the west coast of North America into Central America (Levi 1968). It has been reported from a variety of habitats, including dense perennial vegetation, dry grassy hillsides, vegetable gardens, roadside and deciduous woods margins, and areas adjacent to streams, ponds, and swamps (Gertsch 1979). Observations on the general life habits, systematics, and distribution of *A. aurantia* and related species were summarized by Levi (1968). Other workers have reported on the biology of this species, including overwintering behavior and ecology (Enders 1974, 1977; Riddle & Markezich 1981; Howell & Ellender 1984; Heiber 1985). Minimal information is available, however, concerning the nature and degree of overwintering mortality. Adults and juveniles of *A. aurantia* do not typically survive the winter, even in the southern United States. Adult females of this species produce egg cases containing many hundreds of eggs in late summer and fall. The eggs hatch during winter and the spiderlings remain in the egg case until spring (Tolbert 1976). The present study examines the overwintering survivability of *A. aurantia* egg cases in old fields and roadside margins of Washington County, Mississippi.

METHODS

In January of 1985, nine sites were selected within the Delta Experimental Forest (DEF) located 3.0 km north of Stoneville, Washington County, Mississippi. Four of the sites (Sites 1, 6, 8 and 9) were roadside margins that averaged 1.0–2.0 m in width and had varied plant communities. Sites 2, 3, 4, 5, and 7 were old field successional habitats that ranged from a relatively small field (10 × 100 m, site 4) to an area 2.0 km long and 100 m wide (site 7). Mixed tall forbs (e.g., *Solidago* sp. and *Aster pilosus*) predominated. All sites were within an area (3.5 km × 1.0 km) of the DEF bounded on three sides by soybean, cotton, or fallow fields.

At each site, egg cases of *A. aurantia* were detected by walking parallel linear routes and visually searching the vegetation. Each egg-case location was marked by a 0.5 m strip of red and white flagging tape, with a unique alpha-numeric code written on the tape in indelible ink. To minimize attraction of birds to the colored tape and its associated egg case, the tape was attached

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to vegetation 0.5–1.0 m distant from the egg case. Data were recorded for each egg case and included condition, height above ground, vegetation substrate, degree of exposure, and number of adjacent egg cases within 2.0 m. Marked egg cases were monitored at 30-day intervals in February and March and at 15-day intervals in April and May. At each monitoring, the condition and possible mortality cause(s) were determined. Tolbert (1976) concluded that damage exceeding 10% of the surface area or subsequent disappearance of the *Argiope* egg case was attributable to bird predation. The same criterion was used in our field evaluations. There is no indication, from a search of the literature or from our own observations, that mammal predation is a significant mortality factor in this type of situation. Damage that involved less than 10% of the egg case surface was attributed to insects. This category also was designated when insect emergence holes were detected.

In January 1985, 235 egg cases of *A. aurantia* were located; 120 were marked for future field observations and 115 were removed for laboratory observation. Each collected egg case was placed in a plastic 8 oz.(235 ml) cup with an organdy screen cover held in place by lids from which a 5.0 cm diameter circle had been removed. Cups were then placed outside the laboratory in a screened enclosure with a rain cover. These conditions approximated the temperature and humidity regimens experienced by egg cases that remained in the field. In January 1986 and 1987, field surveys for egg cases were conducted at the same sites as in 1985; however, egg cases were not collected.

RESULTS

Field Observations:—Eighteen percent of the 120 egg cases marked in January 1985 showed previous damage, apparently caused by birds. By mid-February, the percent of damage caused by birds to these egg cases had increased to 64%. In late May, 97% of the egg cases either had been extensively damaged by birds or had disappeared altogether. The remaining 3% of field egg cases in 1985 showed evidence of either insect parasitization or predation.

On one occasion in 1985, we observed actual bird damage to an egg case. During the morning of 19 February, a male House Sparrow, *Passer domesticus domesticus*, was seen removing the contents of a previously undamaged egg case. The bird was startled by our approach and took flight with the eviscerated egg case clasped in its beak and strings of material trailing behind as it disappeared from view.

In mid-January 1986, 27% of the 143 detected egg cases showed evidence of bird damage. In mid-January 1987, all of the 13 detected egg cases showed evidence of bird damage. Over all sites, egg case density also declined during the three survey years. In 1985, density averaged > 5 egg cases per 30 square m. In 1986, this had decreased to slightly > 1.0 egg case per 30 sq. m. In 1987, only 13 egg cases were located within all 9 sites and averaged < 0.1 egg case per 30 sq. m.

Laboratory Observations.—*A. aurantia* spiderlings emerged from all but one of 115 egg cases retained in enclosures from January to June of 1985. Total emerged spiderlings from egg cases (n = 114) was 23,840; range per egg case: 1 (extensively damaged egg case) to 1212 (completely undamaged egg case). The mean emergence from the 114 egg cases was 341 (±81 SE) spiderlings. Thirty-five of the 115 field-collected egg cases were initially damaged by birds. Eventual emergence of spiderlings from these egg cases ($\bar{x}$ = 55 ±17 SE) was considerably less than from insect-damaged egg cases ($\bar{x}$ = 134 ±32 SE) and from undamaged egg cases ($\bar{x}$ = 456 ±148 SE).

During enclosure observations, more than 4700 non-host arthropods also emerged from the 115 egg cases (Table 1). Two species of wasps (Hymenoptera) comprised 83.7% of all emerging non-host arthropods, and one species of fly (Diptera) comprised an additional 14.5%. These three species were: the ichneumonid wasp, *Tromatobia rufopectus* (Say), the eulophid wasp, *Pediobius brachycerus* (Thomson), and the chloropid fly, *Pseudogaurax signatus* (Loew).

Thirty-eight (33%) of the 115 egg cases reared in enclosures were parasitized by *T. rufopectus* ($\bar{x}$ = 6.8 ±1.9 SE *T. rufopectus* pupae per egg case). Only one adult of this species emerged, however, because 258 of the 259 *T. rufopectus* pupae were parasitized by *P. brachycerus*. This hyperparasite produced more than 3700 individuals from the 258 host pupae ($\bar{x}$ = 14.4 ±5.1 SE per pupa). Seven additional species of Hymenoptera also were found in the examined egg cases (Table 1). Of these, only the eupelmid, *Arachnophaga scutata* Gahan, and the eulophid, *Tetrastichus* sp., are known parasites of spider eggs (Eason et al. 1967).

The chloropid fly, *P. signatus*, is an obligate

Table 1.—Arthropods associated with 115 egg cases of *Argiope aurantia* in 1985 in Washington County, Mississippi. * Less than 1%.

Taxon	Percent occurrence in egg sacs	Number of individuals
Psocoptera	*	1
Coleoptera		
Carabidae		
Calleida decora Fab.	*	1
Stenolophus dissimilis DeJ.	*	1
Hydrophilidae		
Cercyon sp.	2	2
Lathridiidae		
Corticaria sp.	3	3
Mycetophagidae		
Litargus sp.	*	1
Rhyncophoridae		
Lixus concavus Say	*	1
Diptera		
Chloropidae		
Pseudogaurax signatus (Loew)	43	687
Lepidoptera		
Arctiidae		
Lithosiinae	2	2
Noctuidae		
Palthis asopialis Guenee	*	1
Hymenoptera		
Braconidae		
Agathis sp.	*	1
Eulophidae		
Pediobius brachycerus (Thomson)	30	3713
Pnigalio sp.	*	1
Tetrastichus sp.	*	1
Eupelmidae		
Arachnophaga scutata Gahan	*	1
Formicidae		
Tapinoma sessile (Say)	*	20
Ichneumonidae		
Itoplectus conquistor (Say)	2	2
Tromatobia rufopectus Cr.	33	259
Pteromalidae		
Pteromalus sp.	*	1
Araneae		
Araneidae		
Eustala cepina (Walck)	*	1
Dictynidae		
Dictyna sp.	*	1
Dictyna hentzi Kaston	2	2
Philodromidae		
Philodromus sp.	*	1
Salticidae		
Eris marginata (Walck)	*	1
Hentzia sp.	2	2
Maevia sp.	*	1
Metaphidippus sp.	5	6
Metaphidippus galathea (Walck)	4	4
Phidippus audax Hentz	*	1
Phidippus clarus Keys	6	27
Tutelina sp.	*	1
Total		4746

predator of spider eggs (Heiber 1984). In 1985, 43% of the enclosure egg cases produced adult *P. signatus* flies. However, only 26 egg cases were attacked singly by this fly; an additional 23 egg cases were attacked by both *P. signatus* and *T. rufopectus*.

Other workers have indicated possible predation of *A. aurantia* eggs by lepidopterous larvae (Heiber 1984, Austin 1985). In our study, two arctiid larvae (subfamily Lithosiinae) were found within the confines of damaged egg cases (Table 1). This subfamily is known to feed only on lichens (Holland 1968). One noctuid moth, *Palthis asopialis* Guenee, emerged from an extensively damaged egg case. Its pupal case and numerous fecal pellets were recovered from within the egg case, suggesting that spider eggs or egg case material had served as food for the larva. Six species of Coleoptera were found in association with *A. aurantia* egg cases. Only one, the carabid beetle *Calleida decora* Fab., is a known predator; however, it was not observed feeding on spider eggs or spiderlings.

Eleven species of spiders, representing nine genera and four families, were obtained from field-collected *A. aurantia* egg cases in the laboratory. These spiders probably were secondary invaders that entered holes made by insects or birds. In one instance, an egg case and dead female of the salticid, *Phidippus clarus* Keyserling,

were found in a damaged *A. aurantia* egg case. Subsequently, 20 *P. clarus* spiderlings emerged on 2 April, followed on 3 May by 412 *A. aurantia* spiderlings. Other spiders have been observed feeding on *A. aurantia* spiderlings in the egg case (Tolbert 1976). We, however, observed no such interspecific predation by spiders.

DISCUSSION

Sources of mortality to overwintering spider eggs can be partitioned into abiotic and biotic parameters. In the southeastern United States, abiotic factors (e.g., weather) are considered of minor importance to winter survival of *A. aurantia* spiderlings inside egg cases (Tolbert 1979; Riddle 1980). Biotic factors (e.g., predation and parasitization) are postulated to have a more profound affect on survival (Auten 1925; Eason et al. 1967).

Birds have been recorded as a major group of predators of orb-weaving spiders on their webs (Marples 1969; Robinson & Robinson 1970; Blanke 1972; Waide & Hailman 1977), including *A. aurantia* (Horton 1983). Birds have also been implicated as a major source of mortality for overwintering arboreal spiders (Gunnarson 1983). Bird predation on spider egg cases and their contents, however, has been mostly documented by anecdotal or circumstantial evidence. Several studies estimated rates of bird predation on orb-weaving spider egg cases that ranged from 7–42% (Enders 1974; Tolbert 1976; Heiber 1984). These studies, however, were conducted only in the fall of each observation year; continued observations into the spring probably would have produced higher incidences of bird predation, perhaps approximating the 100% values observed during our study. During the January to May period of our investigation, birds were foraging both for food and for nesting materials. The local bird density was also increasing during this period, as summer residents were returning and migrants were passing through on the way north. These factors suggest that the level of bird predation on egg cases that we observed may be both typical for such situations and comparable with the results of other investigations.

Egg cases of *A. aurantia* that are damaged by birds provide nesting sites and sheltered habitats for many arthropod species, including other spiders. Many of these associated species are predators or scavengers and may consume host spider eggs or spiderlings. Conversely, they also may consume other predators or parasites of spiders and consequently reduce the overall impact of such organisms on *A. aurantia* eggs and spiderlings. Our data does not allow a determination of the net effect of predator/scavenger arthropods associated with egg cases on the population dynamics of *A. aurantia*.

The level of egg-case parasitization demonstated by *T. rufopectus* in 1985—33%—is in general agreement with values found in previous studies (e.g., 21.5%, Enders 1974; 26.3%, Tolbert 1976; 36.1%, Heiber 1984). *T. rufopectus* is a well known parasitoid of spider eggs and was first described by Cresson (1870) from *A. aurantia* egg cases. It attacks *A. aurantia* eggs by inserting its long ovipositor through the outer cover of the egg case into the flocculent layer. Wasp eggs are deposited on or near the host egg mass and the emerging wasp larvae make their way to the host eggs and burrow into the mass to feed. *P. brachycerus*, a parasitoid of *T. rufopectus*, does no known damage to spider eggs or spiderlings (Peck 1985).

Previous studies have shown the chloropid fly, *P. signatus*, to be a fairly common parasitoid of *A. aurantia* eggs (Enders 1974; Tolbert 1976; Heiber 1984, 1985). However, parasitization values observed during our study were 3–4 times greater than those found previously (Tolbert 1976; Heiber 1984). *P. signatus* oviposits on egg case surfaces, whereupon after fly egg hatch the larvae force their way through the outer covering into the host egg mass (Kessel & Kessel 1937; Hickman 1970). Heiber (1984) found that the level of successful parasitization of *P. signatus* increased significantly when it attacked egg cases already damaged by other parasitoids or predators. These data suggest that prior egg case damage may be an important factor in successful parasitization by this chloropid fly.

The egg cases of *A. aurantia* are assumed to have evolved to protect their contents from one or more mortality factors. It is apparent from our study, however, that these structures have not prevented considerable mortality to their contents caused by bird damage or by parasitization. These two mortality factors, when added to subsequent mortality of spiderlings in the egg case caused by other agents, may be the major determinants of *A. aurantia* population density in old field and margin habitats. On the other hand, bird predation or parasitization typically

does not cause complete mortality in affected egg cases. The number of survivors from such egg cases, combined with those from unaffected egg cases, may be sufficient to maintain population levels of *A. aurantia* in a particular area. Because of the large-scale removal of egg cases from our field sites for laboratory study, the subsequent decline in *A. aurantia* populations cannot be definitively ascribed to either natural or investigator-associated parameters. Determining the relative importance of various mortality factors associated with *A. aurantia* egg cases awaits further experimentation.

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THE EFFECT OF THE COPULATORY PLUG IN THE FUNNEL-WEB SPIDER, *AGELENA LIMBATA* (ARANEAE: AGELENIDAE)

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ABSTRACT. Some females of the funnel-web spider, *Agelena limbata* multiply mate. After copulation, males make a visible copulatory plug which covers the female's genital opening. I assessed the effect of copulatory plugs on the fertilization success of second males, by conducting double mating experiments, using fertile and sterilized males in sequence. When females copulated with only one fertile male, more than 90% of their eggs were fertilized. Some males deposited complete plugs and others incomplete plugs. The relative size of the males to females and absolute male size affected the completeness of plugs. Complete plugs prevented another male's insemination completely, but incomplete plugs allowed insemination by second males. In general, first males had higher fertilization success than second or later males, and copulatory plugs enhanced the first male's advantage.

In many taxa, after mating, the male deposits a copulatory plug that is thought to prevent intromission by other males. This is known in insects (Drummond 1984; Matsumoto & Suzuki 1992), mammals (Martan & Shepherd 1976), snakes (Devine 1975), ticks (Oliver 1974) and spiders (Levi 1959; Jackson 1980; Robinson 1982).

In spiders, there are several reports on the presence of an amorphous secretion-like material blocking the epigynum of just-mated females functioning to prevent intromission by a second male. Other mechanisms for preventing fertilization by second males include the breaking off of the embolus tip in the female's genitalia (*Argiope*, *Nephila*), or the sticking of the cap that normally cloaks the virgin male's embolus tip in some Araneidae (Lopez 1987). Copulatory plugs are considered an adaptive strategy in relation to paternity assurance in spiders (Austad 1982). However, plugs are generally not 100% effective in preventing further mating (Eberhard 1985). Jackson (1980) presented evidence that some secondary mates of females could remove the plug deposited by the first mate.

The funnel-web spider *Agelena limbata* is an annual species with a conduit spermatheca in which there are two separate genital openings: one for copulation and one for oviposition. Some females of *A. limbata* are polyandrous, and males secrete an amorphous material blocking the epigynum of just-mated females.

To understand the evolution of copulatory plugs, their effects must be assessed. In this paper, the effect of copulatory plugs on fertilization success in the funnel-web spider, *A. limbata* was examined by conducting double fertilization experiments, in which one male was sterilized by exposure to γ-rays of Co60.

METHODS

The spiders.—The funnel web spider *A. limbata* is an annual spider commonly distributed in Japan. Females deposit one or two egg sacs under their webs in September after the males disappear, and they protect the sacs for a few weeks before death. The web of this species consists of a flat sheet with an attached funnel extending into twigs of the surrounding vegetation. The sheet has no adhesive properties. After the final molt, the male spider leaves his web and starts his search for mates. Courtship behavior and copulation are performed in the daytime; the duration of copulation is about thee hours (193 ±63 min; mean ±S.D.) (Masumoto 1991).

Field observations.—Observation of the mating behavior of *A. limbata* was conducted from July to September, 1988 and 1989 at the Kyushu University campus, located east of Fukuoka city, Japan. Webs in the study area, located on trees less than 2 m above the ground, were marked and observed daily. In 1988, each web was visited daily in a predetermined order at 3 h intervals from 0900 to 2100 h. In 1989, each web

was visited daily at 1 h intervals from 0900 to 1500 h. Unmarked spiders found in the study area were captured whenever possible. Each spider was brought to the laboratory, anesthetized with CO_2 gas, and individually marked on the dorsal surface of the abdomen with a color marking pen. Within the day, the marked spiders were brought back to the entrance of their original web after another anesthetization. Spiders cohabiting with mates were not disturbed so as not to disrupt their mating behaviors. After the mating season from 1988 to 1992, females were collected to determine the condition of any copulatory plugs.

Laboratory experiments.—Sub-adult spiders were collected in June and July in "Aburayama Observation Park of Nature", Fukuoka, Japan. They were reared in plastic boxes (32 cm × 19 cm or 19 cm × 11 cm). Day length and temperature were almost similar to field conditions. Bees were given to females as a food every four days, a mealworm was supplied to males every week, and water was sprayed on both sexes every four days.

After spiders matured, I measured the cephalothorax width of individuals. Mating experiments were conducted in the morning because in this species mating is diurnal (Masumoto 1991). All experiments were started at between 0800–1000 h and lasted for at least six hours. Each individual was used only one time a day. Individual males chosen at random were released into a box containing a virgin female. After copulation, the genitalia of the females were examined to determine the condition of the copulatory plug. For some females, new males were introduced every day until a secondary copulation occurred.

To determine the fertilization success of secondary mates, double fertilization experiments were conducted using sequential matings of sterilized and fertile (non-treated) males. Males were collected in the field while immature and, after maturation, sterilized by exposure to 7 krad γ-ray of Co60. The behavior of sterile males did not seem to differ from that of unsterile males. Sterlized males were allowed to mate with virgin females, and after copulation occurred, the shape of copulatory plug was recorded. In some cases, after successful mating with a sterile male, a fertile (untreated) male randomly chosen was allowed to mate with the same female. In these cases, males were replaced everyday until the second copulation occurred. The reverse experiment was also conducted with sequential matings of fertile (non-treated) and sterilized males. Females started to deposit their eggs in late August. In late September, the number of eggs and juveniles was counted. Values are represented as means ± SE.

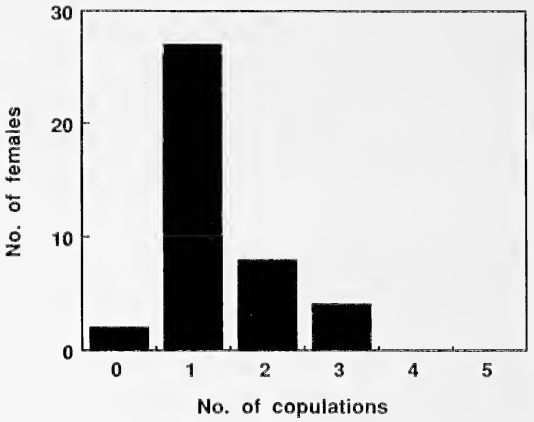

Figure 1.—The distribution of the total number of copulations of marked females through the mating season in 1989 and 1990.

RESULTS

Field observations.—To assess the number of males which courted or copulated with a female, I used data on 41 females which were monitored from virginity to the end of mating season in each year. The end of mating season means the date when the last copulation in field was observed in each year (23 August in 1988 and 21 August in 1989). Females were courted an average of 3.76 ± 2.12 times [4.10 ±0.37 (n = 29) in 1988, 2.92 ±0.66 (n = 12) in 1989] and copulated an average of 1.34 ±0.73 times [1.24 ±0.13 (n = 29) in 1988, 1.58 ±0.23 in 1989 (n = 12)]. Of 39 females which copulated, 12 (30.8%) copulated with an additional male (Fig. 1).

Variation of copulatory plugs.—During the first half of copulation, the male used only one of the palps for insemination. After this, he changed the position of the female which was laying on the web, and he used another palp to inseminate during the last half of copulation. After copulation, all males made a copulatory plug which was secreted from the palps. Some plugs were classified as complete; these covered the female genital opening completely. Others were classified as incomplete; these covered only a portion of

Table 1.—Mean cephalothorax width of males and females, mean ratio of male cephalothorax width to female cephalothorax width, and mean age of males when he first copulated with a virgin female according to condition of copulatory plugs. Values are means ± SE. * Mann-Whitney *U* test.

	Complete plug	Incomplete plug	*z**	*P**
n	31	19		
%	62.0%	38.0%		
Mean cephalothorax width of males (mm)	4.87 ± 0.06	4.67 ± 0.09	2.08	0.038
Mean cephalothorax width of females (mm)	4.79 ± 0.08	4.91 ± 0.09	1.02	0.307
Mean ratio of male cephalothorax width/female cephalothorax width	1.02 ± 0.02	0.96 ± 0.02	2.06	0.039
Mean age of males (days)	15.4 ± 0.7	14.0 ± 1.1	1.53	0.126

the female genital opening. Among 50 untreated virgin males, 31 (62.0%) made complete plugs and 19 (38.0%) of them made incomplete plugs on the first copulation with virgin females.

To assess the cause of variation of the copulatory plugs, I analyzed the relation between the classification of copulatory plugs and relative male size to female size (male cephalothorax width/female cephalothorax width), maximum cephalothorax width of males and females, and male age (Table 1). The mean cephalothorax width of males, and the ratio of male to female cephalothorax width, was greater in males that made complete plugs than in males that made incomplete plugs.

To evaluate the variation of plugs in field, I collected 20 females who were protecting their egg sacs at the end of the mating season. Of 20 females collected, 13 (65%) had complete copulatory plugs in their genitalia and the other 7 (35%) had incomplete plugs.

Sperm usage pattern.—Most eggs of singly-mated female hatched, and the proportion of eggs hatched was not different between females with complete and incomplete plugs. Most sperm were sterilized by the radiation treatment because no eggs hatched when females copulated with sterile males. I could not obtain data about fertile male/sterile male double copulations. When plugs were complete, only the first male's sperm were used in fertilizing eggs. But when plugs were incomplete, the second male's sperm were used for fertilizing 62.9 % of eggs (Table 2).

From the observation of 19 cases of pre-copulatory behavior with non-virgin females (in 10 cases, complete plugs; in 9 cases, incomplete plugs), I found that before insemination of females with incomplete plugs, five second males removed the copulatory plug deposited by previous males, but that four second males did not remove the copulatory plug which was too small to cover the epyginum. Males hooked incomplete plugs with the palp and pulled the plug out. But no male could pull out any complete plug. After removal of an incomplete copulatory plug, males started insemination and covered the genital opening of the female with a new plug after insemination. In seven females which initially had incomplete plugs and then copulated with another male, five of them received complete

Table 2.—Proportion of hatched eggs per female in the experiments with sequential mating of sterilized and fertile males in the spider *Agelena limbata*. Sample number is indicated in parentheses. Values are means ± SE. * Mann-Whitney *U* test.

Mating regime		Proportion hatched			
First male	Second male	Complete plug	Incomplete plug	*U**	*P**
Fertile	—	94.0 ± 5.3% (14)	90.0 ± 9.1% (5)	37	ns
Sterile	—	0.0 ± 0.0% (3)	0.0 ± 0.0% (3)		
Fertile	fertile	88.1 ± 11.9% (4)	93.0 ± 7.1% (4)	8.5	ns
Sterile	fertile	0.0 ± 0.0% (4)	62.9 ± 11.4% (6)	24	<0.01
Fertile	sterile	100.0 ± 0.0% (4)	—		

plugs in their genitalia after the second mating. Plugs did not come out by themselves even after oviposition.

DISCUSSION

From data obtained in field, about 70% of females copulated with a male only once. So first males had a mating advantage compared to the second or later males. But 30.8% of females remated with the next courting male in the field. The reason why some females copulate more than once is unknown in *A. limbata*. Watson (1991b) hypothesized that in the sierra dome spider, *Linyphia litigiosa*, the second mating is important for females as bet-hedging against a cryptic or unexpressed deleterious character present in the first male's genes. Re-mating with another male may be advantageous for some females in *A. limbata*.

There are no externally visible plugs in *Linyphia litigiosa* (Watson 1991a) and in *Frontinella pyramitela* (Austad 1982). In *L. litigiosa*, Watson (1991a) suggested that internal plugs would have to be quite subtle and sections of epigyna have not revealed any plugs, and that fertilization success of some secondary mates is high, although on average first mate sperm priority exists.

Females of *A. limbata* have a conduit spermatheca in which there are separate openings for entry and departure of sperm on opposite sites of the spermatheca. A conduit system has been thought to encourage a 'first-in/first-out' bias in sperm precedence favoring first males (Austad 1984; Watson 1991a). But when second copulations of females with incomplete plugs were successful, the proportion of eggs fertilized by the first male was reduced: second mates were able to fertilize 62.9% of eggs in the double fertilization experiments. Thus in *A. limbata*, though the mechanism of sperm competition of this spider is unknown, first male sperm precedence does not occur despite females having a conduit spermatheca; and gross spermathecal morphology is inadequate to explain sperm priority patterns as Watson (1991a) suggested.

When first mates do not make a complete copulatory plug, their fertilization success is reduced. Thus in *A. limbata*, the copulatory plug is very important in assuring first male sperm advantage. Incomplete plugs tended to be made by relatively small males, though the statistic was marginally significant. Smaller males may be unable to fill the genital opening of females with a plug secretion, but the precise cause of incompleteness of the copulatory plug in *A. limbata* is unclear.

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STING USE IN TWO SPECIES OF *PARABUTHUS* SCORPIONS (BUTHIDAE)

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ABSTRACT. Scorpions sometimes capture and crush prey with their pedipalps and do not use their sting to inject venom. Experiments were conducted to test the hypothesis that sting use is selective, resulting in conservation of venom. Sting use in relation to prey size and activity was studied in two African scorpions, *Parabuthus liosoma* and *P. pallidus*. Restrictive use of the sting was observed in both species. Decreased use of the sting occurred with decreasing size/resistance of the prey. Also, prey were not stung immediately after being seized, but only after resisting capture. The scorpions did not sting non-resistant prey. These results support the notion that sting use depends upon the size, morphology and resistance of the prey as determined during initial interactions with the scorpion.

Scorpions are notorious for their stinging behavior and powerful venoms. Sting use plays an important role in prey capture and defense (Vachon 1953; Cloudsley-Thompson 1958; Stahnke 1966). As yet, there have been no controlled and quantitative studies of sting use, but investigators have suggested a variety of factors that may be correlated with sting use. It appears that scorpions with large, powerful pedipalps seldom use the sting, while species with small, slender pedipalps readily sting their prey (Stahnke 1966; Baerg 1961; McCormick & Polis 1990). Casper (1985) proposed an ontogenetic change in sting use by *Pandinus imperator* Koch. Young individuals stung prey readily, while older and adult individuals were never observed to employ the sting. Similar results were reported by Cushing & Matherne (1980) for *Paruroctonus boreus* Girard. Le Berre (1979) noted decreased sting use with smaller prey in *Buthus occitanus* Amor., and similar observations were reported for other species (Pocock 1893; Vachon 1953; Cloudsley-Thompson 1958; Baerg 1961; Bücherl 1971; Polis 1979).

The purpose of this study is to examine sting use during prey capture by two East African buthids, *Parabuthus liosoma* Hemprich & Ehrenberg and *Parabuthus pallidus* Pocock. Both species used their stings selectively, depending upon the size, morphology and resisting behavior of the prey. Results are discussed in terms of the costs and benefits of venom injection during prey capture.

METHODS

Natural history.—*Parabuthus liosoma* and *P. pallidus* are found in several countries in East Africa (Probst 1973). Adults of the former species are of medium size for scorpions and have a yellow to yellowish-red body, except for part of the cauda and telson which are dark red/brown. They have small, slender pedipalps and a thick, powerful cauda. Similar coloration and morphology is present in *P. pallidus*, but these are slightly smaller and lack the darkened distal part of the cauda. There are no previous reports on the life history or behavior of these species.

Materials.—Individuals of *P. liosoma* and *P. pallidus* were collected in the vicinity of Isiolo, Kenya in May and June, 1988. The animals were found in the same semi-arid area under stones along roadsides, but no more than one scorpion was ever found beneath a single stone. The substrate consisted of compacted sand with occasional grass and bushes.

The scorpions were taken to Norway, where 11 individuals of *P. liosoma* and 12 individuals of *P. pallidus* were used in the experiments. The specimens were of unknown age and ranged in length (pro- and mesosoma) from 18–32 mm ($\bar{x}$ = 25.1 mm, *P. liosoma*) and 13–31 mm ($\bar{x}$ = 21.3 mm, *P. pallidus*).

Specimens were kept individually in terraria (32 × 20 cm), with a substrate of sand and some stones. The temperature was held at 24–30 °C, and the light/dark period was 10:14 hr. Water was provided weekly by misting. Animals were

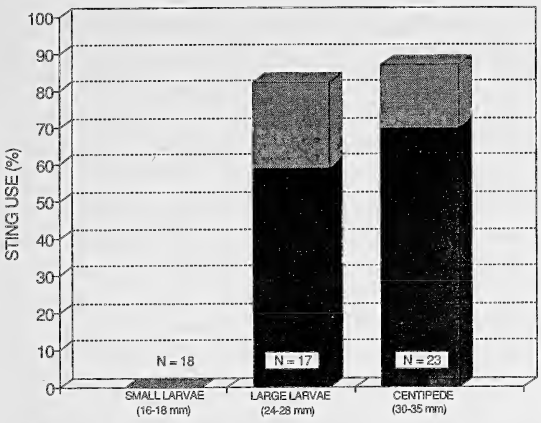

Figure 1.—Sting use against three different prey types in *Parabuthus liosoma*. The whole columns represent total sting use, whereas the dark shaded areas show the percentage successful sting use (see text for further explanations). "N" denotes the number of trials.

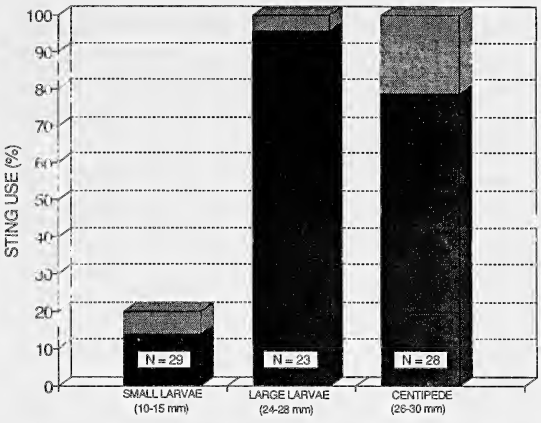

Figure 2.—Sting use against three different prey types in *Parabuthus pallidus*. The whole columns represent total sting use, whereas the dark shaded areas show the percentage successful sting use (see text for further explanations). "N" denotes the number of trials.

not fed except when tested. Only animals active on the surface in the dark period were selected for experiments. This appeared to be a useful indication of hunger, since they usually responded rapidly when prey were offered.

For testing, the scorpions were transferred to an observation terrarium (25 × 25 cm) with a sand floor. They were given one hr for acclimation before prey was introduced. Data on all activities were collected by direct observations under low intensity red light that is apparently not visible to scorpions (Machan 1968). All observations were made during the fall 1988 and spring 1989. Results were tested using a sign test (Lehner 1979).

Experiment 1.—Sting use was compared after presentation of three different types of prey which differed in size and morphology. These were small (10–18 mm) and large (24–32 mm) larvae of *Tenebrio molitor* Linne and a centipede, *Lithobius forficatus* Verhoeff (26–35 mm). Insect larvae and centipedes were seen in the scorpions' habitat in Kenya, and thus are probably natural prey for the two *Parabuthus* species.

After the acclimation period, a live prey was introduced to the test scorpion, and if accepted, observations were continued until ingestion was started. The scorpions were allowed to complete ingestion before they were transferred back to their terrarium. If the prey was not accepted by a scorpion, the test was discontinued, and the animal was returned to its terrarium.

Experiment 2.—Sting use against non-resistant prey was investigated by introducing freshly killed *Tenebrio* larvae (29–35 mm) to the scorpions. The larvae were presented by moving them with forceps on the substrate near the scorpion pedipalps.

RESULTS

Prey were subdued in two ways. In 43.3% of the trials (n = 138), scorpions grasped the prey with one or both pedipalps and then pulled the prey to the chelicera and began ingestion without use of the sting. In the remaining trials, the scorpions used the sting to subdue the prey. In some of the latter trials, scorpions did not succeed in penetrating the prey integument; these scorpions either attempted to sting again or stopped stinging and devoured the prey alive. These cases were recorded as sting use, whereas cases with penetration of the integument were recorded as successful sting use.

Sting use in *P. liosoma*.—In this species, the sting was used significantly less ($P < 0.001$) against small larvae than with the two prey of larger size (Fig. 1). There were no significant differences in sting use against the large larvae and the centipedes. Attempts were made to sting both of the large prey types in about 85% of the trials, and the sting use was successful in 58.8% (larvae) and 69.6% (centipedes) of the trials.

Sting use in *P. pallidus*.—Individuals of this species attempted to sting the small larvae significantly less ($P < 0.005$) than the two large prey types (Fig. 2). Small prey were stung in 20.1% of

the trials, whereas the use of the sting against large larvae and centipedes was observed in all trials. Sting use was successful in 13.8% of the trials with small larvae, 95.7% with large larvae and 78.6% with centipedes.

Assessment of prey.—Prey were usually not stung immediately after being seized by the pedipalps. Immediate sting occurred in 14.7% (*P. liosoma*) and 26.3% (*P. pallidus*) of the trials in which the sting was used. In most trials, the sting was used only after the prey struggled and resisted capture. In several trials, the scorpions attempted to subdue the prey with the pedipalps for several minutes before finally using the sting.

Sting use against non-resistant prey.—The scorpions quickly grasped large, dead *Tenebrio* larvae which were moved on the substrate near the pedipalps. Sting use were never observed in any of these cases. This is significantly different from sting use with live prey of the same size (*P. liosoma*, $P < 0.005$, $n = 9$; *P. pallidus*, $P < 0.001$, $n = 13$).

DISCUSSION

The results provide evidence that scorpions restrict use of the sting and thereby conserve venom. This is supported by the observations that they displayed decreasing sting use with decreasing size/resistance of prey (Figs. 1, 2). In most trials when the prey were stung, scorpions did not sting the prey immediately after seizing it (a period of prey assessment occurred before use of the sting). Moreover, no scorpion stung non-resistant prey (dead larvae), even though they were large in size. This also supports the notion that the scorpion evaluates the struggle and resistance activity of the prey before stinging it.

The possibility of restrictive sting use was suggested from earlier observations of several scorpion species (Pocock 1893; Rosin & Shulov 1963; Le Berre 1979; Polis 1979; Cushing & Matherne 1980), but experimental evidence was lacking before the present investigation. Williams (1987) suggested that scorpions more commonly eat their prey alive or crush them by pedipalps than inject venom. A similar pattern of restrictive venom use was reported for some other predators. The ant, *Camponotus maculatus*, uses the venom spray differently for large and small prey (Dejan 1988), and some snakes reportedly vary the quantity of venom used for different prey (Gennaro et al. 1961; Allon & Kochva 1974).

Sting use in *P. liosoma* and *P. pallidus* probably depends upon the size, morphology and resistance of the prey. Large prey (large larvae) and prey with powerful mouthparts (centipedes) were stung frequently by both *Parabuthus* species, whereas small prey (small larvae) and non-resistant prey (dead larvae) were seldom stung. The size and resistance activity of the prey was evaluated by the *Parabuthus* in an assessment period shortly after capture.

A restrictive sting use in *P. liosoma* and *P. pallidus* is probably advantageous because the use of the sting and the following venom renewal is expensive from an energetic point of view. This was not examined, but it is a reasonable hypothesis since the venom contains a mixture of water, salt, proteins and other complex molecules (Simard & Watt 1990).

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A NEW SPECIES OF *VAEJOVIS* (SCORPIONES, VAEJOVIDAE) FROM WESTERN ARIZONA, WITH SUPPLEMENTAL NOTES ON THE MALE OF *VAEJOVIS SPICATUS* HARADON

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ABSTRACT. A new species of *Vaejovis* is described from two localities along the Colorado River in western Arizona. The species is related to *Vaejovis spicatus* Haradon, to which it is compared. The first known male specimen of *V. spicatus* is briefly described, and comments on its hemispermatophore are provided. Hemispermatophore morphology of *V. spicatus* suggests a close phylogenetic relationship of these two species with members of the genus *Serradigitus*, although they lack several features considered diagnostic for that genus.

In 1974 a peculiar species of *Vaejovis* was described from the Little San Bernadino Mountains in southern California. Haradon (1974) named this species *Vaejovis spicatus* because it was the only vaejovid known to possess a distinct, spinoid subaculear tubercle. In the early 1980s, Dr. Oscar Francke brought several interesting specimens to my attention that were collected along the Colorado River in western Arizona. Like *V. spicatus*, these specimens bore the strong, spinoid subaculear tubercle. After studying them, however, it became apparent that they differed from *V. spicatus* in some significant features. It is part of the purpose here to describe the Arizona specimens as a new species.

More recently, the first known male specimen of *V. spicatus* was made available for study. Because males of both forms were unknown, it seems appropriate to provide some brief descriptive notes on its morphology. Although the specimen was in very poor condition, dissection of the hemispermatophore revealed some interesting characters that shed new light on the relationships of these two species to other members of the family.

Vaejovis mumai, new species
(Figs. 1–7)

Type data.—Adult holotype female from Gold Road, Black Mountain, Mohave Co., Arizona on 17 May 1969 (M. A. Cazier, et al.). Deposited in the American Museum of Natural History (0. F. Francke Collection).

Etymology.—This species is dedicated to Dr. Martin Muma for his many contributions to American arachnology.

Distribution.—Known from several localities in western Arizona.

Diagnosis.—*Vaejovis mumai* is most similar to *V. spicatus*. *Vaejovis mumai* and *V. spicatus* are the only two vaejovid species possessing a distinct, spinoid subaculear tooth on the telson vesicle (*Serradigitus joshuaensis* has a conspicuous tubercle, but not a spinoid tooth). *Vaejovis mumai* may be easily distinguished from *V. spicatus* because the pedipalp chela fixed finger has only five subrows of denticles along the cutting margin (in *V. spicatus*, the fixed finger has six subrows). The lateral inframedian carinae are more highly developed in *V. mumai*, being more or less complete on both I and II and extending over the posterior ½ of segment III. The ventrolateral and ventral submedian carinae in *V. mumai* are also stronger and more coarsely denticulate than in *V. spicatus*. The carinae of the pedipalp chelae are somewhat stronger in *V. mumai*. There are also some distinct morphometric differences, as *V. mumai* is a larger species (females 24.5 mm *vs.* 16–17.5 mm) and has more robust pedipalps and metasomal segments. The following ratios demonstrate the differences in the latter features (values for the holotype and paratype females of *V. spicatus* given in parentheses; based on Haradon's measurements): Pedipalp femur length/width, 3.16 (3.33–3.45); pedipalp patella length/width, 2.95 (3.29–3.31); pedipalp chela length/width, 3.45 (3.50–3.61); pedipalp chela fixed finger length/carapace length, 0.70 (0.76–0.77); metasoma III length/width, 0.86 (0.96–1.0); and metasoma V length/width, 1.27 (1.65–1.67).

Vaejovis mumai may be easily distinguished

from *V. jonesi* Stahnke, another small yellowish *Vaejovis* in northern and western Arizona that it superficially resembles, by possessing the subaculear tooth on the telson, by having metasomal segments I–III wider than or as wide as long (not with II–III distinctly longer than wide), and by having trichobothria *ib* and *it* of the chela fixed finger subbasal (rather than at the extreme base of the fixed finger). *Vaejovis mumai* also has only five subrows on the pedipalp chela fingers, whereas *V. jonesi* always has six subrows.

Description.—Adult (female) 24.5 mm in length. Base color yellow to golden brown, without contrasting dusky markings; metasoma and pedipalps with orange tinge. Carapace moderately coarsely granular. Tergites more finely granular. Sternite VII with pair of weak, crenulate lateral keels. Pectinal tooth count 13 in males, 11 in females. Proximal pectinal tooth on each side ovoid in shape and lacking sensilla.

Metasoma: segments I–III distinctly wider than long; V 1.27 times longer than wide. Segments I–IV: Dorsolateral carinae strong, crenulate; terminal denticles enlarged, spinoid. Lateral supramedian carinae strong, crenulate; terminal denticles on I–III enlarged spinoid, on IV widely flared. Lateral inframedian carina on I complete, strong, irregularly crenulate; on II almost complete, weak and granular anteriorly, moderate and crenulate posteriorly; on III present on posterior one-half, moderate, crenulate; on IV absent. Ventrolateral carinae moderate to strong, serratocrenulate; ventral submedian carinae on I weak, granular; on II-IV moderate, serratocrenulate. Setation of dorsolateral carinae 0:1:1:2; ventral submedian carinae 3:3:3:3. Dorsal and lateral intercarinal spaces with scattered coarse granules. Segment V (Fig. 1): Dorsolateral carinae strong, irregularly crenulate; lateromedian carinae moderate, granulose; ventrolateral and ventromedian carinae strong, crenulate to serratocrenulate; all surfaces moderately, coarsely granular. Telson vesicle slightly granular with distinct, pointed, subaculear tooth (Fig. 1).

Pedipalps: Trichobothrial pattern (Figs. 2–7) Type C, orthobothriotaxic (Vachon 1974). Femur (Fig. 2) tetracarinate, with dorsal surface lightly granular. Patella (Figs. 3–4) dorsointernal, internal, and ventrointernal carina strong, crenulate; dorsoexternal and ventroexternal carinae moderate, unevenly granular. Chela (Figs. 5–7) with dorsal marginal carina strong, granulose; dorsointernal carina strong, crenulate; dorsal secondary, digital, and ventroexternal carinae moderate, smooth; fixed finger (Fig. 7) with primary denticle row divided into five subrows, movable finger with six such subrows; trichobothria *ib* and *it* of fixed finger situated between base of finger and the sixth inner accessory granule. Ratio of pedipalp chela length/width 3.45; of fixed finger length/carapace 0.70; of movable finger length/metasoma V length 1.21.

Measurements of Holotype (in mm to nearest 0.05 mm): Total length, 24.5; carapace length, 3.50; mesosoma length, 8.50; metasoma length, 9.15 (I length/width, 1.35/1.80; II length/width, 1.50/1.80; III length/width, 1.60/1.85; IV length/width, 2.20/2.10; V length/width, 2.60/2.05); telson length, 3.35 (vesicle length/width/depth, 2.55/1.85/1.30; aculeus length, 0.80); pedipalp length 11.60 (femur length/width, 3.00/0.95; patella length/width, 3.25/1.10; chela length/width/depth, 5.35/1.55/1.65; fixed finger length, 2.45; movable finger length, 3.15).

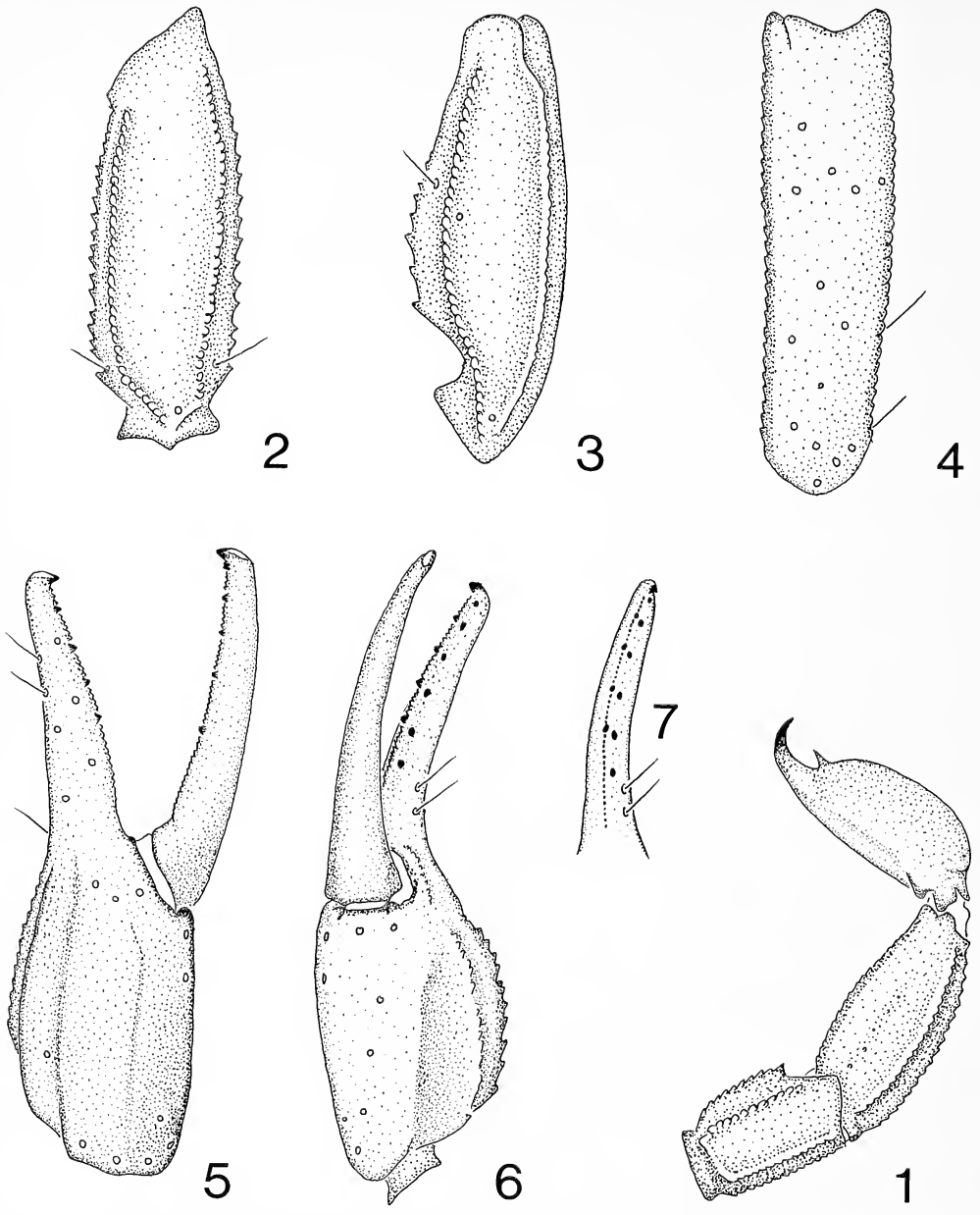
Variation.—Only a single adult, the holotype female, was available for study. The juvenile specimens (middle instars) differ primarily in coloration, being very pale yellow, and in having the cuticle more weakly sclerotized.

Comments.—Several attempts to re-collect this species by myself and colleagues at "P" Mountain have met with failure. The species is probably very uncommon and/or exhibits infrequent surface activity during the year.

Specimens examined.—**U.S.A.**: *Arizona*: Mojave Co.: Gold Road, Black Mountain, 17 May 1969 (M. A. Cazier, et. al.), 1 holotype female, 2 juvenile paratypes (AMNH-OFF); Gold Road (under rock), 15 March 1976 (M. A. Cazier, O. F. Francke), 1 juvenile paratype (AMNH-OFF); "P" Mountain, near Parker, 14 March 1976 (M. A. Cazier, O. F. Francke), 1 juvenile paratype (AMNH-OFF).

COMMENTS ON THE MALE OF *VAEJOVIS SPICATUS* HARADON, 1974

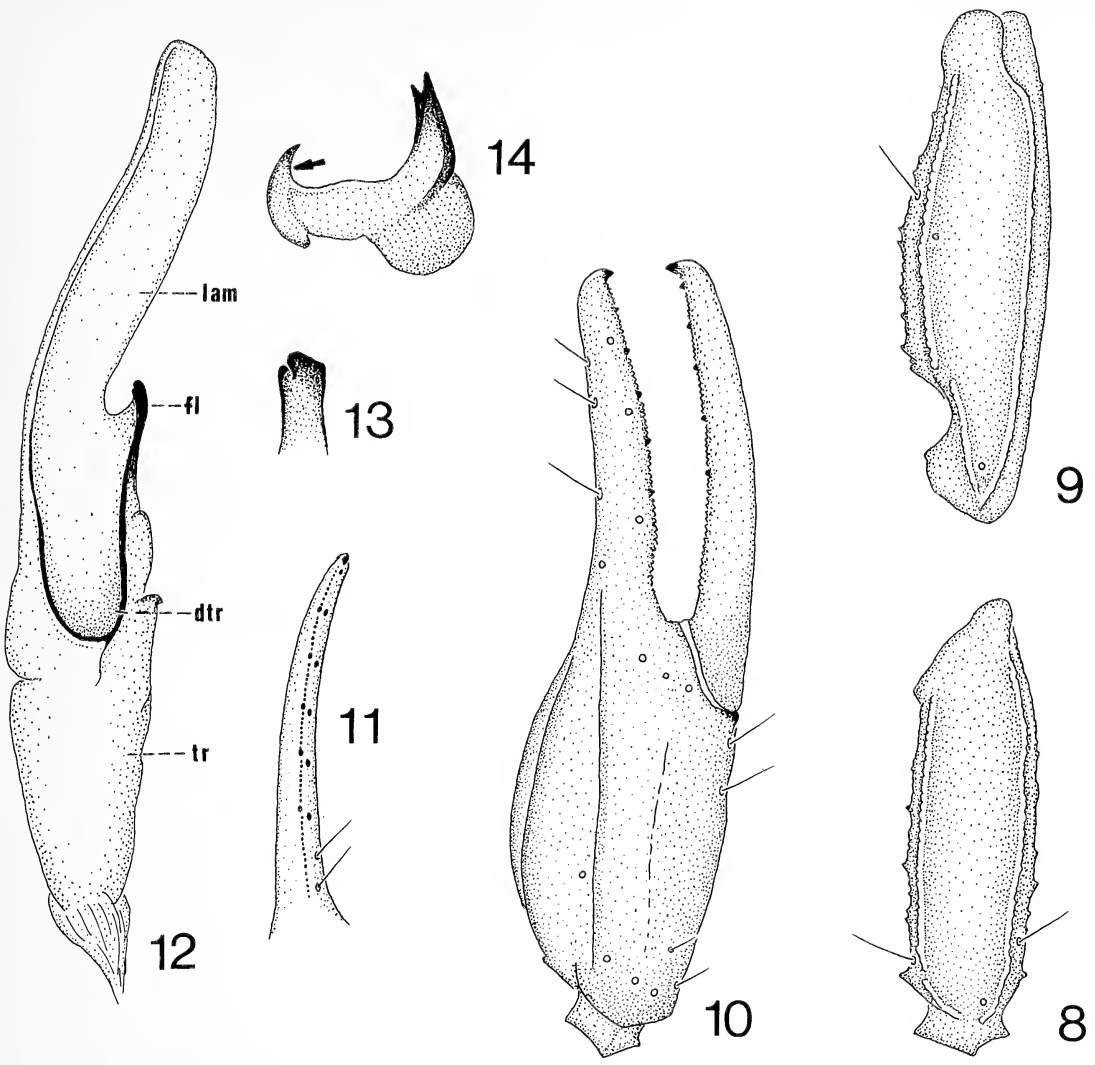
The original description of *Vaejovis spicatus* Haradon was based on five specimens (two of which were adult females) collected from Berdoo Canyon in the Little San Bernadino Mountains of Riverside Co., California. In sorting through material on loan from the California State University at Long Beach, I found a male specimen of *V. spicatus* from Pleasant Valley, Joshua Tree National Monument, Riverside Co., California, collected in a pitfall trap on August 27, 1966 by E. L. Sleeper and S. L. Jenkins. Because the male of this species is previously unknown and its



Figures 1–7.—Morphology of holotype female of ***Vaejovis mumai***, new species: 1, left lateral aspect of metasomal segments IV and V and telson; 2, dorsal aspect of pedipalp femur; 3, dorsal aspect of pedipalp patella; 4, external aspect of pedipalp patella; 5, external aspect of pedipalp chela; 6, ventral aspect of pedipalp chela; 7, cutting margin of pedipalp chela fixed finger, showing dentition and placement of trichobothria *ib* and *it*.

morphology proved quite interesting, it is important to add some descriptive notes here.

The male compares to the female as follows: granulation of the carapace, tergites, and metasoma as well as the carination of the pedipalps and metasoma are similar to that of the female. A few morphometric differences are as follows: metasoma V is considerably wider than in females (V length/width = 1.44); the pedipalp femur (Fig. 8) and patella (Fig. 9) are slightly more slender than in the female (femur length/width = 3.53 *vs.* 3.33–3.45; patella length/width = 3.50 *vs.* 3.29–3.31); but the pedipalp chela (Fig. 10) is slightly more robust, with a chela length/width ratio of 3.36 rather than 3.50–3.65. The pectinal tooth count of the male is 12–12. The pedipalp



Figures 8–14.—Morphology of male of *Vaejovis spicatus* Haradon: 8, dorsal aspect of pedipalp femur; 9, dorsal aspect of pedipalp patella; 10, external aspect of pedipalp chela (note subtle scallop at base of fixed finger); 11, cutting margin of pedipalp chela fixed finger, showing dentition and placement of trichobothria *ib* and *it*; 12, dorsal aspect of right hemispermatophore; 13, ental aspect of lamellar flange; 14, ventral aspect of "sperm plug" of hemispermatophoric capsule (note the smooth margin at the arrow). *lam* = distal lamina; *fl* = flange; *tr* = trunk; *dtr* = dorsal trough of distal lamina.

chela fixed finger has a slight basal scallop (Fig. 10), but there is no corresponding lobe on the movable finger; this leaves a space between the fingers when they are closed. The fixed finger, with its six subrows of denticles, is shown in Fig. 11.

Measurements of the specimen are as follows (in mm, to nearest 0.05 mm): Total length, 15.90; carapace length, 2.20; mesosoma length, 4.95; metasoma length, 6.65 (I length/width, 0.95/1.10; II length/width, 1.05/1.10; III length/width, 1.10/1.15; IV length/width, 1.50/?; V length/width, 2.05/1.40); telson length, 2.10 (vesicle length/width/depth, 1.50/1.05/0.75; aculeus length, 0.55); pedipalp length, 6.95 (femur length/width, 1.95/0.55; patella length/width, 2.15/0.60; chela length/width/depth, 2.85/0.85/0.95; fixed finger length, 1.60; movable finger length, 2.05).

The hemispermatophore is illustrated in Figs. 12–14. The specimen and its hemispermatophores were in very poor condition, so both hemispermatophores were prepared for study as

described by Sissom et al. (1990) in order to obtain a composite drawing. Once the entire hemispermatophore was drawn, attempts were made to dissect the capsular region to discern its fine structure. These attempts proved futile, as the capsular structures fragmented. However, it was still possible to make some important observations. The hemispermatophore is very slender, with the distal lamina noticeably longer than the trunk (Fig. 12; the ental margin of the distal lamina bears a broad flange that terminates some distance away from the base of the distal lamina (Fig. 12); the flange (Fig. 13) is distally bilobed; and the ental process of the inner lobe of the capsule does not bear hooklets (Fig. 14).

In light of the structure of the hemispermatophore, the earlier interpretation of *V. spicatus* as a member of the *Vaejovis nitidulus* group (Sissom & Francke 1985) now seems inappropriate. *Vaejovis spicatus* and *V. mumai* seem more properly allied to *Serradigitus* (but not included therein) based on the following evidence. First, the presence of the flange along the ental margin of the distal lamina bearing a distally-positioned bilobed termination is shared between *V. spicatus* and *Serradigitus*, as well as with several other vaejovid groups (*Syntropis macrura* and species of the *Vaejovis eusthenura*, *punctipalpi*, and *intrepidus* groups; Sissom 1991). The presence of the flange, the distal position of the bilobed termination, and the shape of that termination are all hypothesized to be apomorphic. This condition does not occur in other vaejovids. Second, the proximal pectinal tooth on each side in the female (of *V. mumai*, at least) is ovoid and lacks peg sensilla, a feature previously thought to occur only in *Serradigitus* (Sissom & Stockwell 1991). And third, although fixed finger trichobothria *ib* and *it* are not positioned at the sixth inner accessory denticle or beyond (a character uniting all *Serradigitus* spp.), they occupy a subbasal position midway between the extreme base of the finger and the sixth inner accessory denticle. In this respect, they differ from members of the *V. nitidulus* and *mexicanus* groups, in which the trichobothria are at the extreme base of the finger. Lastly, it should be noted that placement of *V. spicatus* and *V. mumai* within the genus *Serradigitus* does not seem appropriate because the terminal denticles on the pedipalp chela fingers in these species are not enlarged and clawlike and the primary denticle row is not conspicuously serrate. Both of these features are regarded as diagnostic of *Serradigitus*.

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I am grateful to Dr. Oscar Francke for allowing me to examine the type specimens of *Vaejovis mumai* and to Dr. Wojciech J. Pulawski of the California Academy of Sciences for allowing me to examine a paratype specimen of *V. spicatus*. Dr. E. L. Sleeper kindly loaned me a large number of scorpion specimens from collection of the California State University at Long Beach, one of which turned out to be the male specimen of *V. spicatus* described herein. Marshall Hedin and T. Yamashita attempted to collect this species at "P" Mountain at my request, and I am grateful for their efforts. Page charges for this article were paid by the Department of Biology and Geosciences at West Texas State University. Finally, I wish to thank Drs. Victor Fet and John T. Hjelle for their reviews of the manuscript.

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ON THE IDENTITY OF *IDEOBISIUM TIBIALE* BANKS (NEOBISIIDAE: PSEUDOSCORPIONES: ARACHNIDA)

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ABSTRACT. The holotype of *Ideobisium tibiale* Banks, from Colorado, USA, is redescribed. This species is transferred from *Microcreagris* Balzan to *Cryptocreagris* Ćurčić (Neobisiidae). The diagnosis of the genus *Cryptocreagris* is emended.

The pseudoscorpions originally assigned to the genus *Microcreagris* Balzan 1892 and inhabiting North America north of Mexico have been partially revised by Ćurčić (1984, 1989). While undertaking a further revision of this genus, it became clear that *Ideobisium tibiale* Banks, 1909, was erroneously assigned to the genus *Microcreagris* by subsequent researchers (Hoff 1958; Harvey 1991). The results of the study of the unique holotype of *M. tibialis* are presented here. In addition, this study should further stimulate an analysis of the taxonomic rank of all other North American pseudoscorpions currently assigned to "*Microcreagris*".

METHODS

The holotype specimen was borrowed from the Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, Massachusetts, USA. The specimen, mounted on a slide, was thoroughly examined. Terminology basically follows that used by Ćurčić (1984, 1989).

Family Neobisiidae Chamberlin, 1930

Genus *Cryptocreagris* Ćurčić, 1984

Diagnosis (emendations italicized).—Galea with apical branchlets. Abdominal sternites VI and VII each with 2 anterior discal setae. *Sternite VIII with 2 median setae only slightly anterior to other marginal setae (not typical discal setae!).* Male genital area: sternite II with a group of median and posterior setae, sternite III with a group of anterior, some intermediate, and a series of posterior setae. Female genital area: sternite II with a group of small setae on each side of the midline, sternite III with a row of posterior setae.

Manducatory process with 4 *or 5* (*occasionally 3 or 6*) setae. Femur and chelal palm of pedipalps *smooth or* with inconspicuous granulations. Trichobothriotaxy: *esb* distal to *eb*; *ist-isb-ib* clustered on finger base; *it* and *et* located distally on finger tip; *esb* nearer to *it* than to *ist*; *st* slightly closer to *t* than to *sb* (*or equidistant from these*); *sb* slightly closer to *b* than to *st* (*or equidistant from these*).

Leg IV: tibia, basitarsus, and telotarsus with 1 tactile seta each.

Type species.—*Microcreagris laudabilis* Hoff.

Subordinate taxa.—*Cryptocreagris laudabilis* (Hoff), *C. magna* (Banks), and *C. tibialis* (Banks).

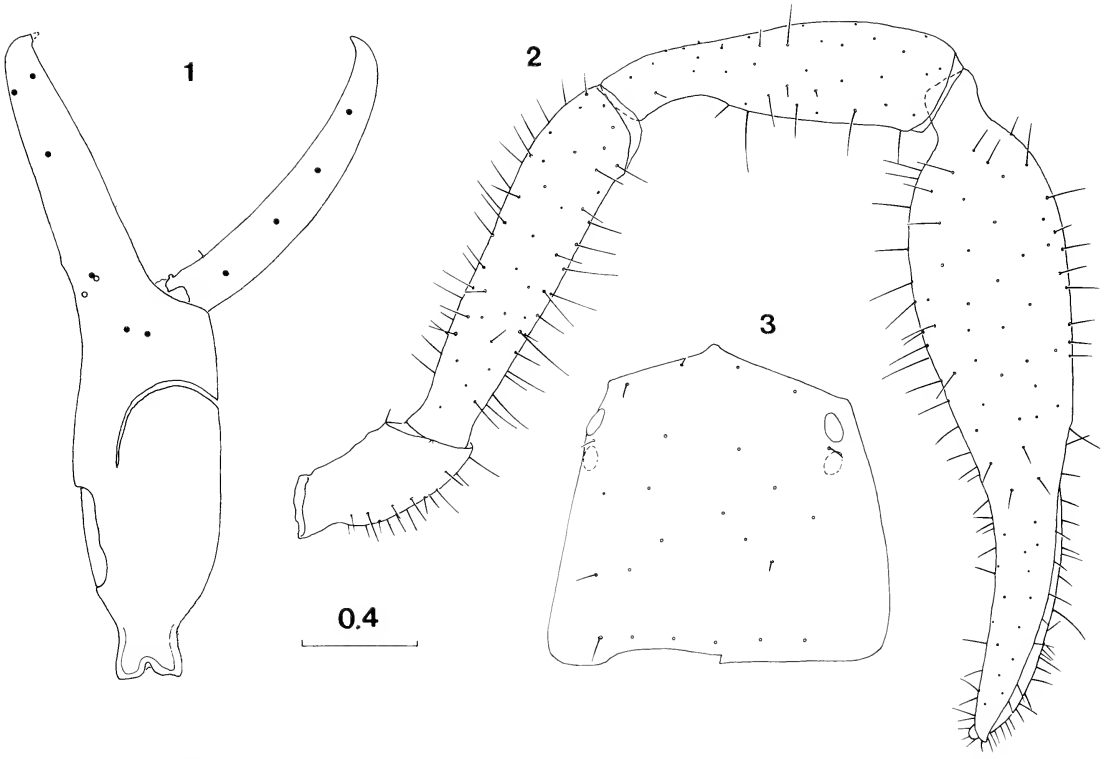
Cryptocreagris tibialis (Banks), new combination (Figures 1–6)

Ideobisium tibiale Banks, 1909:306
Microcreagris tibialis (Banks): Harvey, 1991:345 (full synonymy)

Description.—Epistome low and rounded apically, carapace with 4 + 4 + 4 + 6 + 6 = 24 setae. Anterior eyes with flattened lenses, posteriors spot-like (Fig. 3). Galea with terminal branchlets (Fig. 5). Flagellum with 8 anteriorly pinnate blades.

Tergites I–X with 6–9–9–12–13–?–?–12–12–11 setae. Male genital area: unknown. Female genital area (Fig. 4): sternite II with a group of 6 or 7 setae on either side of midline, sternite III with 23 posterior setae and 5–7 setae along each stigma. Sternite IV with 19 marginal setae and 4–6 setae along each stigma, sternite V with 14 setae. Sternites VI and VII each with 16 or 17 setae and 2 anterior discal setae each. Sternite VIII with 15 setae and 2 setae only slightly anterior to other marginal setae (these two setae are *not* the typical discal setae!).

Pedipalps (Fig. 2): manducatory process with 4 long setae. Fixed chelal finger with asymmetrical distal teeth, gradually becoming square-



Figures 1–3.—*Cryptocreagris tibialis*, holotype female. 1, pedipalpal chela (trichobothrial pattern); 2, pedipalp (trichobothria omitted); 3, carapace. Scale in mm.

topped and eventually slightly asymmetrical. Movable chelal finger with teeth similar in form and size to those on the fixed finger; only a few distal teeth asymmetrical. Trichobothriotaxy as illustrated (Fig. 1).

Leg IV: tibia, basitarsus, and telotarsus with 1 tactile seta each (Fig. 6).

Measurements (mm).—Body length 4.80. Carapace 1.41/1.365. Chelicera 0.84/0.41, movable finger length 0.53, galea 0.13. Pedipalps: coxa 1.04, trochanter 0.88, femur 1.71/0.38, tibia 1.60/0.43, chela 2.98/0.69, chelal palm 1.44, fixed finger 1.54. Leg IV: total length 5.515, coxa 0.78, trochanter 0.60/0.29, femur 1.495/0.35, tibia 1.47/0.185, basitarsus 0.49/0.14, telotarsus 0.68/0.14.

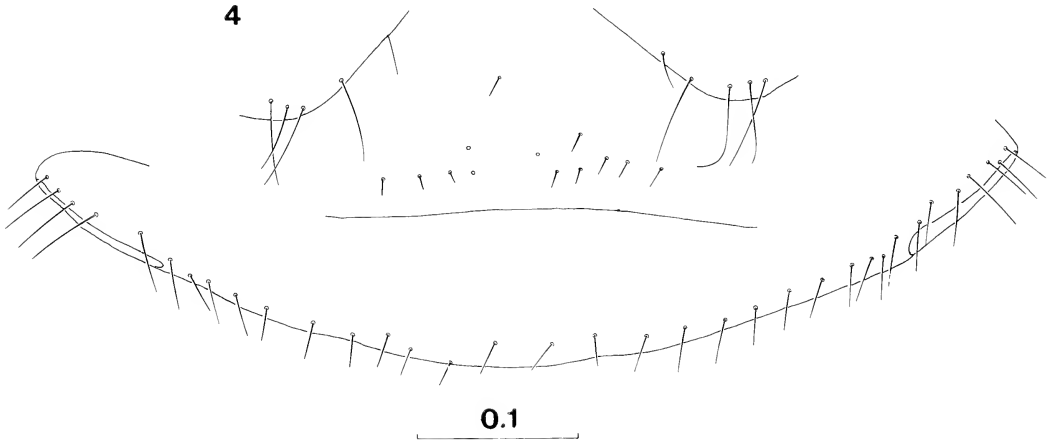
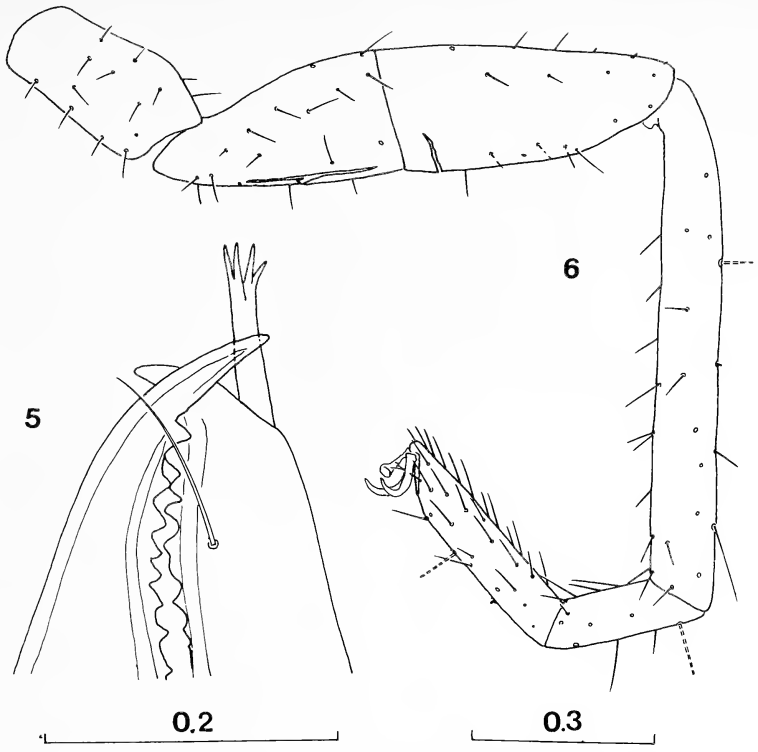


Figure 4.—*Cryptocreagris tibialis*, holotype female. Genital area. Scale in mm.



Figures 5, 6.—*Cryptocreagris tibialis*, holotype female. 5, cheliceral fingers; 6, leg IV. Scales in mm.

Tactile seta position/podomere length ratios: tibia IV 0.345, basitarsus IV 0.20, telotarsus IV 0.29.

Distribution.—Colorado, USA.

Remarks.—Hoff (1956) found that the type specimens of *C. laudabilis* showed "considerable agreement with the original description" of *C. tibialis*, which favored his assignment of these two species to the same genus. Interestingly, Hoff (1961) studied three more nymphs (two protonymphs and one deutonymph) from Florissant and from near Gothic, Colorado, USA, respectively. He found that they resembled both *C. laudabilis* and *C. tibialis*, and he pointed out that the similarity "may be only in generic characteristics". Both conclusions of Hoff (1956, 1961) support the assumption that *C. laudabilis* and *C. tibialis* are congeneric.

The material of *C. laudabilis* (Hoff) and *C. magna* (Banks) has been described elsewhere (Ćurčić 1984, 1989).

Specimen examined.—Holotype female (WM 1213.01001), from USA: Colorado: Florissant; 8,000 ft., July-August (year and collector lacking on label).

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THE GENUS *CHILEOGOVEA* (OPILIONES, CYPHOPHTHALMI, PETALLIDAE)

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ABSTRACT. The opilionid genus *Chileogovea* is reviewed and a new species, *Chileogovea jocasta*, from Malleco Province, Chile, described. Some supplementary illustrations and new records from mainland Chile of the type species, *C. oedipus* Roewer, are provided.

The opilionid genus *Chileogovea* was established by Roewer in 1961 for a new species, *Chileogovea oedipus*, from Chepu, Isla de Chiloé, Chile. Roewer's description was sufficient to establish the validity of the new genus, which he placed in the Family Sironidae (the only named family of cyphophthalmids at the time), but omitted important details, such as the form of the male genitalia. In 1970, Juberthie and Muñoz-Cuevas produced a new description and new illustrations, providing information on these characters, and giving a new record from a mainland locality, Nahuelbuta. They noted the resemblance of *Chileogovea* to the New Zealand genus *Rakaia* Forster, and assigned both to the Family Sironidae Simon. In 1980, in a study of the higher classification of cyphophthalmids, I placed the genus *Chileogovea* in the new Family Pettalidae, together with *Rakaia* and the other southern hemisphere cyphophthalmids previously in Sironinae (*Pettalus* Thorell, *Purcellia* Hansen and Sörensen, *Speleosiro* Lawrence, *Parapurcellia* Rosas Costa, and *Neopurcellia* Forster; Juberthie [1988] has named a new genus, *Austropurcellia*, which also belongs in this family). The family is distibuted in South Africa, Sri Lanka, New Zealand and Australia, and Chile.

In 1981, 1985–86, and 1992, Norman Platnick, Oscar Francke and Randall Schuh of the American Museum of Natural History made collecting trips to Chile, as did A. Newton and M. Thayer in 1982. Among their material were examples of *Chileogovea*, including specimens of a new species, and near topotypes and several new mainland records of *C. oedipus*. I thank Dr. Platnick for the opportunity to study these specimens, all of which have been deposited in the American Museum of Natural History (AMNH). James Cokendolpher and Emilio Maury provided helpful reviews of the manuscript.

Specimens were observed, measured, and drawn using a dissecting microscope. The right chelicera, pedipalp, first and fourth legs, and penis were then mounted in glycerine on a microscope slide and examined with a compound microscope outfitted with Nomarski Interference Contrast optics, and measured with an ocular micrometer. All measurements are in millimeters; in the description, measurements of appendage segments are given in order from basal to distal (beginning with trochanter for pedipalps, femora for legs), lengths first, separated from widths by a diagonal stroke, and L/W ratios, if significant, follow in parentheses.

Family Petallidae Shear

Genus *Chileogovea* Roewer

Chileogovea Roewer, 1961:99; type species *C. oedipus* Roewer. Juberthie & Muñoz-Cuevas, 1970:109. Shear, 1980:25. Cekalovic, 1985:8.

Cekalovic (1985) evidently was unaware of the Family Pettalidae, and repeated Roewer's original assignment of the genus to the Family Sironidae, Subfamily Stylocellinae, already recognized as incorrect by Juberthie & Muñoz-Cuevas in 1970.

A redescription of the genus was given in 1970 by Juberthie & Muñoz-Cuevas, based entirely upon the characters of *C. oedipus*, the only species known at that time. The discovery of a second species, *C. jocasta*, requires further emendation of the generic diagnosis as follows.

Coxae 1, 2 free, 3, 4 fused. Eyes absent. Ozophores type 3. Chelicerae (Fig. 3) robust, dorsally crested. Cheliceral fingers with both large and small teeth (Figs. 4, 12). Abdominal sternites 8,

9 free, tergite 9 free. Tarsus 4 entire. Male secondary sexual modifications: adenostyle lamellar, sharply curved (Figs. 8, 14); sternites 5–8 shallowly depressed in midline, or sternites 7, 8 each with pair of paramedian tubercles (mistakenly stated by Shear [1980] to be on 6, 7); anal operculum with or without prominent median ridge; tergite 9 evenly rounded posteriorly or shallowly excavate. Penis (Figs. 9, 10, 15, 16) of *Siro* type.

Distribution.—Central Chile, Concepcíon south to Chiloé.

Notes.—I cleared the posterior ends of males of both species of *Chileogovea* in trypsin, mounted the cleared parts on microscope slides, and examined them under high magnification for gland pores. Sternal gland pores occur in the males of the genera *Huitaca* and *Ogovea* (Family Ogoveidae), and *Troglosiro* (family unknown), while anal gland pores are found in tergite 9 of male Sironidae. Because of the modifications of the sterna I expected to find glands, but none could be detected in either species, and anal glands were likewise missing. Thus the function of the sternal modifications in male *Chileogovea* remains unclear.

The two species of the genus can be separated by means of the diagnosis given below under the description of *C. jocasta*.

Chileogovea jocasta, new species
Figs. 1–10

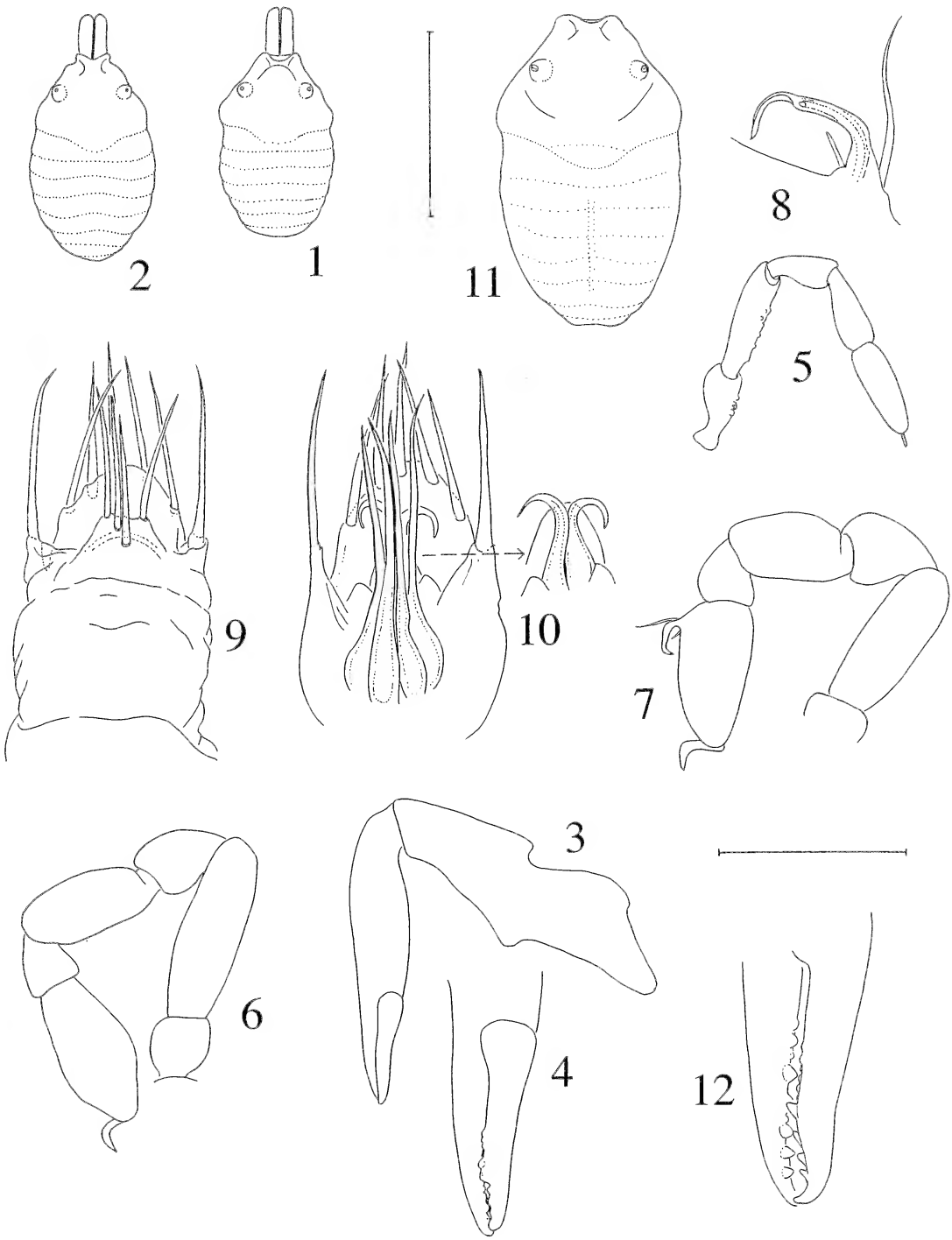
Type data.—Holotype male, paratype female, seven additional paratype males, and nine additional paratype females (AMNH) from Berlese sample of forest litter and moss, montane forest zone, 300 m elevation, Monumento Nacional Contulmo, Malleco Prov., Region IX (de la Araucañia), Chile, collected 31 January 1986 by N. I. Platnick and R. T. Schuh. Additional paratype female (AMNH) from the same locality, but from 425 m elevation, collected 23 January 1985 by N. I. Platnick and O. F. Francke; 32 male and 25 female paratypes (AMNH) from litter Berlese, 560 m elevation, Pata de Gallina, Arauco Prov., Region VIII (Bío Bío), collected 11 February 1992 by N. I. Platnick, P. Goloboff, and M. Ramírez.

Etymology.—Roewer was probably referring to the well known Greek myth in naming his species *oedipus*, though he did not explain his reasons for doing so. I follow suit by naming this new species for another figure from the same myth (the name used as a noun in apposition).

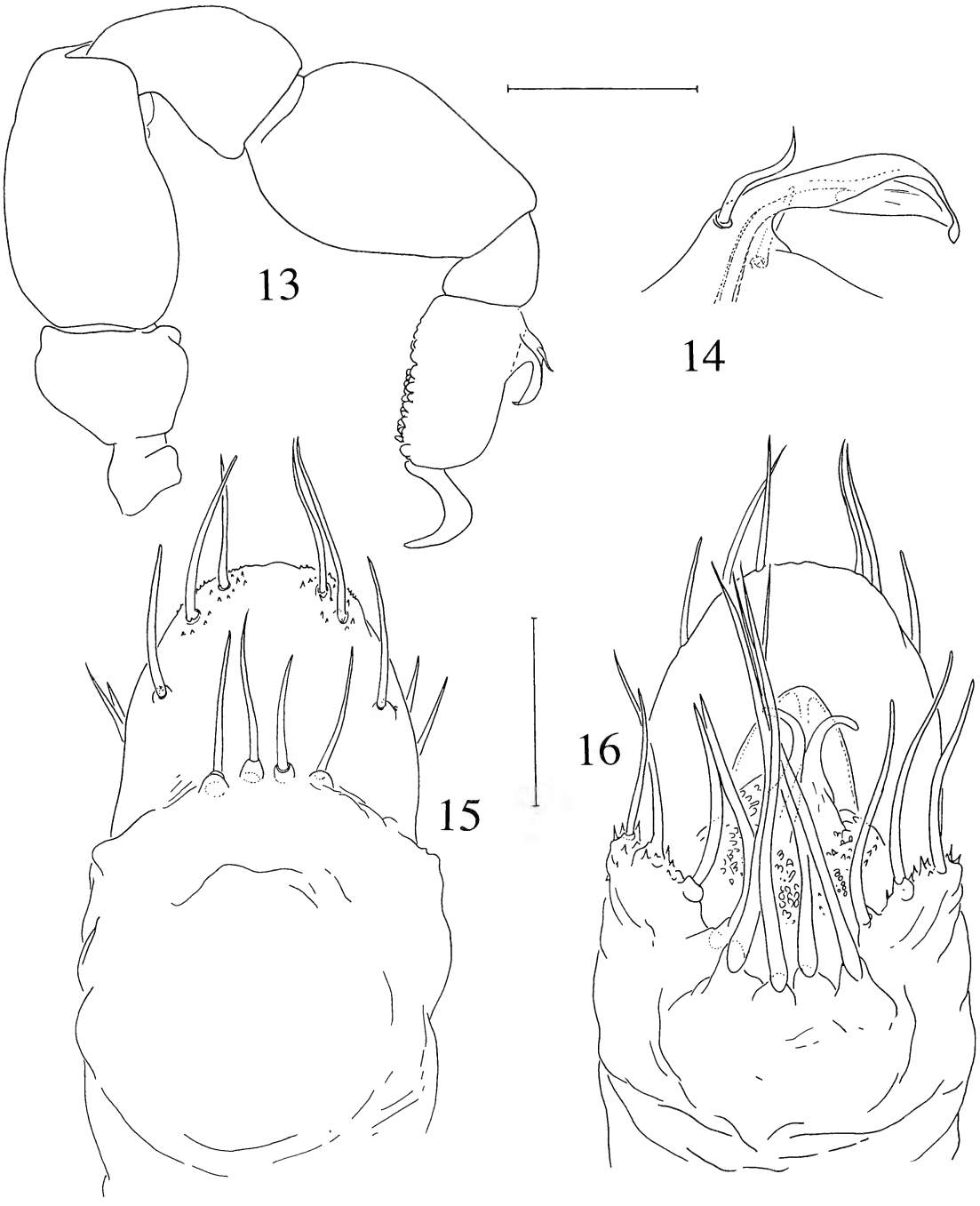
Distribution.—Known only from the type localities.

Diagnosis.—Distinct in numerous characters from *C. oedipus*, the only other known species of the genus. *Chileogovea jocasta* males and females are less than 2 mm long, the males lack conspicuous secondary sexual modifications of the posterior sternites, the adenostyles of males are markedly more slender (Fig. 8), the fourth tibia (Fig. 7) has a L/W ratio of 1.77, and the setation of the penis is reduced (Figs. 9, 10); *C. oedipus* ranges from 2.5 to 3.28 mm long, the males have strongly modified posterior sternites, broad adenostyles (Fig. 14), the fourth tibia (Fig. 13) has a L/W ratio of 1.58, and the penial setae are more numerous (Figs. 15, 16).

Description.—*Male:* Total length, 1.7, greatest width, 1.05, L/W = 1.62. Body (Fig. 1) generally egg-shaped, widest at posterior part of cephalothorax, not dorsoventrally arched as in *C. oedipus*. Dorsum shining, with heavily pebbled microsculpture. Ozophores well removed from cephalothorax margin, directed straight upwards; seen laterally, paler in color than rest of dorsum. Cephalothoracic sulcus distinct laterally, less so near midline; abdominal sulci pronounced. Posterior end of body evenly rounded. Ventral thoracic complex as in *C. oedipus*. Abdominal sternites without conspicious modifications, sternites 6–8 somewhat depressed in midline. Anal operculum without crest. First cheliceral segment (Fig. 3) 0.83 long, 0.26 wide, strong dorsal crest present, heavily pebbled. Second cheliceral segment 0.77 long, 0.14 wide, straight, evenly tapered, fixed finger 0.29 long, 38% length of second cheliceral segment. Cheliceral teeth (Fig. 4) irregular, large and small teeth mixed. Palpal segments (Fig. 5) 0.22, 0.31/0.08, 0.18, 0.20/0.08, 0.25. Legs robust, with heavily pebbled ornamentation. Leg 1 (Fig. 6) segments 0.48/0.15 (3.2), 0.24/0.16, 0.36/0.16 (2.25), 0.16/0.14, 0.39/0.19. Leg 4 (Fig. 7) segments 0.41/0.15 (2.73), 0.22/0.19, 0.32/0.18 (1.77), 0.17/0.17, 0.37/0.18. Adenostyle (Fig. 8) sharply curved, with long, acute tip reflexed to nearly touch dorsal surface of tarsus. Penis in ventral view (Fig. 9) with four ventral setae closely grouped on distinct tubercle; in dorsal view (Fig. 10) with five apical setae slightly removed ventrally from apical margin of dorsal plate, lateral setae single, well separated from dorsal plate, four dorsal setae closely grouped, with bulbous bases; gonopore margins with two long, acute,



Figures 1–12.—(1–10, *Chileogovea jocasta*, n. sp.), 1, dorsum of male; 2, dorsum of female; 3, chelicera of male; 4, cheliceral teeth of male; 5, palpus of male; 6, leg 1 of male; 7, leg 4 of male; 8, adenostyle, 9, penis, ventral view; 10, penis, dorsal view. (11, 12, male *Chileogovea oedipus* Roewer), 11, dorsum; 12, cheliceral teeth. Scales = 1.85 mm for Figs. 1, 2, 11; 0.5 mm for Figs. 3, 5, 6, 7; 0.25 mm for Fig. 4; 0.13 mm for Figs. 8–10, 12.



Figures 13–16.—Male *Chileogovea oedipus*: 13, leg 4; 14, adenostyle; 15, penis, ventral view; 16, penis, dorsal view. Scales = 0.5 mm for Fig. 13; 0.13 mm for Figs. 14–16.

curved fingers with lateral lobes at bases. Color dark blackish brown, dorsally with irregular black streaks in older specimens; legs bright orange-brown.

Female: (Fig. 2). Total length, 1.85 mm. Closely resembling male in all nonsexual characters.

Notes.—One additional male whose penis was dissected had four, rather than five, apical setae.

At all three known localities, this species is syntopic with *C. oedipus*, taken in the same Berlese sample.

Chileogovea oedipus Roewer
Figs. 11–16

Chileogovea oedipus Roewer, 1961:100 (male holotype, male paratype, two female paratypes from Chepu, Isla Chiloé, 850 ft. elevation, mixed evergreen forest; in Senckenberg Museum, Hamburg, not examined); Juberthie & Muñoz-Cuevas, 1970:110.

The excellent and detailed description by Juberthie & Muñoz-Cuevas needs little supplement. However, they did not emphasize the distinctiveness of the posterior paramedian sternal tubercles, which, in most populations, on their median faces are nearly perpendicular to the sternite surface. This face is bordered by a semicircle of small, regular tubercles about one-third the size of the tubercles ornamenting the body. They did not mention at all a single, very much enlarged tubercle situated in the midline of the fourth sternite. This tubercle is in the form of an equilateral triangle with its apex pointing posterior; each side of the triangle is about five times as long as an ordinary body tubercle.

A figure of the dorsum (Fig. 11) of a specimen from a new locality (Rio Negro), and of the cheliceral teeth (Fig. 12), leg 4 (Fig. 13), and adenostyle (Fig. 14) are presented here for comparative purposes. The illustrations of the penises of males from two localities given by these authors were reproduced at small size, and I provide larger figures of the penis of a male from Rio Negro (Figs. 15, 16).

The important differences between this species and the foregoing new one are enumerated above. Probably due to its rather wide distribution (about 750 north-south km), *C. oedipus* shows some variation in both size and penial setation. Both Roewer (1961) and Juberthie & Muñoz-Cuevas (1970) give the length of a male specimen from Chepu as 2.5 mm and the latter gave the length of a female from Chepu as 3.0 mm; I measured a single Chepu male as 2.65 mm long; two females were 2.75 and 2.8 mm long. Juberthie & Muñoz-Cuevas (1970) had a male from Nahuelbuta available but did not give its length; a male from Nahuelbuta examined by me was 3.28 mm long, and males from the Rio Negro region averaged 2.88 mm long. Juberthie and Muñoz-Cuevas (1970) illustrated the penises of males from Chepu and from Nahuelbuta; the Chepu male had three ventral and six apical setae, while the Nahuelbuta male had four ventral and four apical setae. A male from Rio Negro (Figs. 15, 16) shows either five ventral or four (rather than the usual three) lateral setae on one side, and six apical setae. The Estero Nonquen population seems the most divergent. Males differ from those in other populations in having the sternal lobes and the crest on the anal plate reduced; the legs of both sexes are somewhat more slender than in individuals of the same body length from Rio Negro. The penis has four ventral and six apical setae, and the ventral plate has an irregular distal margin. It is possible this population represents a third species, but for now I consider it within the range of variation of *oedipus*.

The penises illustrated by Juberthie & Muñoz-Cuevas, together with the size differences I observed, led me at first to suspect that the Nahuelbuta and Estero Nonquen populations were distinct species, but more careful examination of these and other specimens, as well as comparisons with the new species *C. jocasta*, caused me to conclude that the differences were simply variations in a geographically widespread species.

Specimens examined.—CHILE: Region VIII (Bío Bío) *Arauco Prov.*, Pata de Gallina, 560 m elevation, litter in forest, 11 February 1992, N. I. Platnick (NIP), P. Goloboff, M. Ramírez, 11 males, 4 females; Region IX (de la Araucania), *Concepción Prov.*, Estero Nonquen, 90 m elevation, litter berlese in modified forest, 16 November 1981, N. I. Platnick, R. T. Schuh (RTS), 4 males, 5 females; *Malleco Prov.*, Parque Nacional Nahuelbuta, 1250 m elevation, mossy forest floor litter (*Nothofagus*, *Auracaria*), 19 November 1981, NIP, RTS, male; Monumento Nacional Contulmo, 300 m, wet forest, 31 January 1986, NIP, RTS, 6 males; Region X (de los Lagos), *Llanquihue Prov.*, 13 km west of Rio Negro, 20 m elevation, Berlese of litter from edge of disturbed forest, 24 January 1986, NIP, RTS, 10 males, 9 females; 35 km northwest of Rio Negro, 240 m elevation, Berlese of litter from edge of disturbed forest, 24 January 1986, NIP, RTS, 9 males, 7 females; Lago Chapo, 11.7 km east of Correntoso (site 657), berlese of forest leaf and log litter, 320 m elevation, 16–27 December 1982, A. Newton (AN), M. Thayer (MT), male; 13.5 km east of Correntoso (site 656), window trap in Valdivian rainforest, 310 m elevation, AN, MT, male; berlese of forest leaf and log litter, male, female. *Osorno Prov.*, hills south of Maicolpué, 75 m elevation, wet disturbed forest, 26 January 1986, NIP, RTS, 2 males, 4 females; 10 km east of Bahia Mansa , 15 m elevation, disturbed forest, 30 January 1985, NIP, O. F. Francke (OFF), male, female; Volcán Osorno, 610 m elevation, mature forest, 12 February 1985, NIP,

OFF, male, female; Chincay, 10 km east of Bahia Mensa, 50 m elevation, berlese forest leaf and log litter in secondary Valdivian forest, AN, MT, 3 males, female. *Chiloé Prov.*, Isla de Chiloé, Chepu, elev. 15 m, wet forest, 2 February 1985, NIP, OFF, male, 2 females.

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Manuscript received 28 July 1992, revised 10 December 1992.

1993. The Journal of Arachnology 21:79–80

RESEARCH NOTE

ON THE FEMALE OF *CRYPTOCELLUS GOODNIGHTI* (ARACHNIDA: RICINULEI)

The New World ricinuleid fauna includes two genera, *Cryptocellus* and *Pseudocellus*, occurring in South and North America, respectively, but showing broad sympatry within Central America. The 11 known Central American species of *Cryptocellus*, reviewed by Platnick & Shadab (1981a, b), belong to the *centralis* group, which also extends into Colombia. Of the 11 Central American species, four have been known only from males.

Among a shipment of ricinuleids collected in Costa Rica by Dr. Allen M. Young and recently sent to me for study by Dr. Joan P. Jass of the Milwaukee Public Museum (MPW) were adults of two species. One male of *C. fagei* Cooke & Shadab was taken in a rotten banana stem in cacao at Finca La Lola, near Siquirres (10°06′N, 83°22′W), Limón, Costa Rica on August 9, 1984, and is the first record of that species from Limón Province. Three other males, belonging to *C. goodnighti* Platnick & Shadab, were taken in rotten banana stem slices at Finca La Tigra, near La Virgen (10°24′N, 84°07′W), Heredia, Costa Rica from September 26–28, 1979 and on September 3, 1989. A single female taken at the same locality on September 15, 1978 appears to be the first known female of the latter species, and is described below. I thank Dr. Mohammad U. Shadab of the American Museum of Natural History for providing the illustrations.

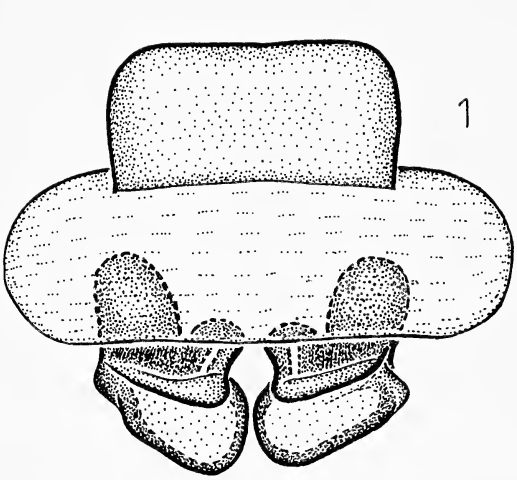
Cryptocellus goodnighti Platnick & Shadab
Figs. 1, 2

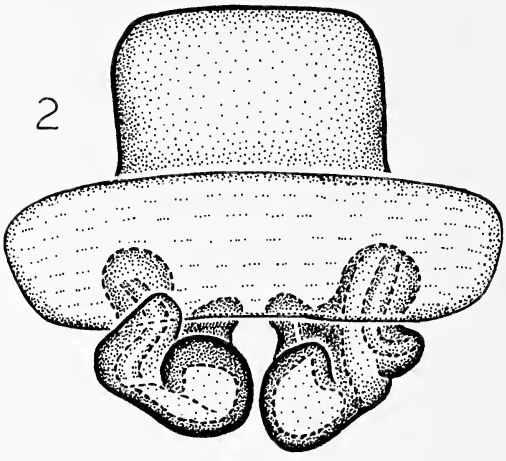
Cryptocellus goodnighti Platnick & Shadab, 1981a: 10.

Diagnosis.—Females can easily be distinguished from those of the other known *centralis* group species by their elongated, tripartite spermathecae (compare Figs. 1, 2 with the illustrations in Platnick & Shadab 1981a, b).

Female.—Total length, excluding pygidium, 5.36 mm. Carapace 1.97 mm long, 2.14 wide near middle of coxae III, where widest, dark red, lateral margins darkest, with small yellow translucent areas at margins opposite front of coxae II; surface coated with strong white setae, relatively uniform in length, with relatively few tubercles largely confined to longitudinal median depression, pair of oblique paramedian depressions occupying about one-fifth of carapace length, and posterior margin. Cucullus 0.94 mm long, 1.17 mm wide, dark red medially with slightly paler margins, bearing long white setae sparsest proximally, with tubercles largely restricted to distal margin; lateral lobes only very slightly protuberant. Left chelicera: movable finger concave posteriorly, not widened transversely, armed with 13 teeth, of which most proximal three, fifth, and tenth reduced to denticles, distal three slightly enlarged; fixed finger armed with five teeth of which most distal is much enlarged, three most proximal reduced to denticles. Sternal region with coxae I not meeting tritosternum; coxae II meeting for almost their entire length, their suture line almost three times as long as that of coxae III; coxae IV meeting along their median surfaces.

Abdomen 3.81 mm long, 1.39 wide near front of tergite 12, where widest, coloration as in carapace except for light orange articular membranes, white setae shorter than on carapace; tubercles restricted to transverse band on tergite 9, anterolateral depressions of median plates, corresponding depressions of sternites 11–13, posteromedian surface of median plate of tergite 11, and throughout length of median one-third of median plate of tergite 12; median plates of tergites 11–13 much wider than long. Pygidium with notch in posterior dorsal margin of basal segment, without notch in ventral margin.





Figures 1, 2.—*Cryptocellus goodnighti* Platnick and Shadab, female, posterior genital lip and spermathecae: 1, anterior view; 2, posterior view.

Palp orange, with first trochanter and tibia lightest; few tubercles on coxae and trochanters, base of femora with cluster of tubercles at base on retromargin; coxae each with two thick white setae posteriorly along inner margin. Leg formula 2431. Legs dark reddish brown with tarsi lightest, coated with thin, long, white setae, with few tubercles concentrated on ventral ridges of tibiae and dorsal ridges of metatarsi and tarsi. Leg measurements are given in Table 1. Second legs slightly widened; femur I about twice, femur II about three times as long as wide. Tarsal claws large, evenly curved. Posterior genital lip and spermathecae as in Figs. 1, 2.

Table 1.—Leg measurements.

Leg	I	II	III	IV	Palp
Coxa	0.66	1.13	0.96	0.90	0.40
Trochanter I	0.53	0.85	0.62	0.75	0.49
Trochanter II	—	—	0.57	0.56	0.41
Femur	1.20	1.98	1.39	1.53	1.01
Patella	0.75	1.21	0.90	0.87	—
Tibia	0.97	1.61	0.85	1.00	1.54
Metatarsus	1.09	1.73	1.09	1.18	—
Tarsus	0.49	1.60	0.77	0.90	0.23
Total	5.69	10.11	7.15	7.69	4.08

Material Examined.—Only specimens mentioned above (MPW).

Distribution.—Known only from northeastern Costa Rica.

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Krafft, B. 1982. The significance and complexity of communication in spiders. Pp. 15–66, *In* Spider Communications: Mechanisms and Ecological Significance. (P. N. Witt & J. S. Rovner, eds.). PrincetonUniversity Press, Princeton.

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Figures 1–4.—*A-us x-us,* male from Timbuktu: 1, left leg; 2, right chelicera; 3, dorsal aspect of genitalia; 4, ventral aspect of abdomen.

Figures 27–34.—Right chelicerae of species of *A-us* from Timbuktu: 27, 29, 31, 33, dorsal views; 28, 30, 32, 34, prolateral views of moveable finger; 27, 28, *A-us x-us,* holotype male; 29, 30, *A-us, w-us,* holotype male; 31, 32, *A-us z-us,* holotype male; 33, 34, *A-us y-us,* male. Scales = 1.0 mm.

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CONTENTS

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Cover illustration: A male *Tetragnatha extensa* from Carlisle, Massachusetts. Original color photo by Joe Warfel of Arlington, Mass. Photograph made with a handheld Olympus OM-1 35mm camera, macro lens, telescoping extension tube and manual flash.

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THE GENUS *TROGLOSIRO* AND THE NEW FAMILY TROGLOSIRONIDAE (OPILIONES, CYPHOPHTHALMI)

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ABSTRACT. The cyphophthalmid genus *Troglosiro* Juberthie, known only from New Caledonia, is made the type of a monobasic new family Troglosironidae, the plesiomorphic sister group of [Pettalidae + Sironidae]. Five new species, *raveni*, *juberthei*, *ninqua*, *tillierorum* and *platnicki*, are described.

Juberthie (1979) described *Troglosiro* as a new genus of cyphophthalmid based on the single species *Troglosiro aelleni* Juberthie, from d'Adio Cave (also known as Grotte de Ninrin-Reu) on the island of New Caledonia. Despite its generic name and the characterization of the species as "cave-dwelling" in the paper's title, *T. aelleni* has no detectable morphological adaptations for a troglobitic existance. Juberthie (1979, 1989) and Shear (1980, 1985) were unable to place the genus in the classification of cyphophthalmids but agreed that it was related to the clade Sironidae + Pettalidae, and while zoogeographically allied to the latter, had more characters in common with the former. In addition, *T. aelleni* has at least three autapomorphies: some of the male abdominal sterna have small, median exocrine gland orifices, the apical setae of the penis are greatly enlarged and basally fused, and the movable fingers of the penis are very large, roughened, and have fimbriate outer margins.

Recent collecting for soil animals on New Caledonia by A. and S. Tillier, and by Norman Platnick and Robert Raven, resulted in the discovery of five new species sharing these apomorphies. Study of this new material has convinced me that *Troglosiro* constitutes the sister-group of Sironidae + Pettalidae, and thus should be placed in its own family, named and diagnosed below.

I am grateful to Drs. Platnick and Tillier for allowing me to study their material, and to Dr. B. Hauser, Natural History Museum, Geneva, Switzerland, for the loan of type material of *Trogolosiro aelleni*. All primary types have been deposited in the Musée National d'Histoire Naturelle (MNHN), Paris. Secondary types, where available, have been deposited in the American Museum of Natural History (AMNH), New York.

Specimens were observed, measured, and drawn using a dissecting microscope. The right chelicera, pedipalp, first and fourth legs, and penis were then mounted in glycerine on a microscope slide and examined with a compound microscope outfitted with Nomarski Interference Contrast optics, and measured with an ocular micrometer. All measurements are in millimeters; in the descriptions, measurements of appendage segments are given in order from basal to distal (beginning with trochanter for pedipalps, femora for legs), lengths first, separated from widths by a diagonal stroke. Length/Width ratios, if significant, follow in parentheses.

Family Troglosironidae, new

Diagnosis.—Distinct from all other cyphophthalmids in the following combination of characters. Penis with apical setae enlarged and fused, movable fingers of penis enlarged and with dentate/fimbriate lateral margins (Figs. 15, 16, 24–28, 43), and sterna of males with 2–4 median exocrine gland pores (Fig. 30).

Type genus.—*Troglosiro* Juberthie 1979, by present designation and monotypy.

Distribution.—New Caledonia.

Remarks.—The new family is named because the genus it contains cannot be placed in any of the existing monophyletic families of cyphophthalmids, and because an integration of the characters of its type genus into the cladistic analysis by Shear (1980) causes it to appear in the cladogram as the sister group of the two families Pettalidae and Sironidae, thus indicating at least a family-level rank for the taxon. The new family is supported by the autapomorphies given in the diagnosis.

Genus *Troglosiro* Juberthie

Troglosiro Juberthie, 1979:222; type species *T. aelleni* Juberthie.

Description.—Coxae 1, 2 free, 3, 4 fused. Eyes absent. Ozophores type 2. Chelicerae (Figs. 2, 10, 18, 31) robust, basal article with (Fig. 18) or without (Fig. 10) dorsal crest. Cheliceral fingers with regular or irregular teeth (Figs. 18, 38). Abdominal sternites 8 and 9, and tergite 9 fused as corona analis. Tarsus 4 entire. Tarsal claws 1, 3, 4 smooth, 2 toothed (Fig. 34). Male secondary sexual modifications: adenostyle lamellar, not curved, acute-triangular, at base of tarsus 4 (Figs. 5, 6, 37, 42). Sternites with 2, 3, or 4 small, median exocrine gland pores (Fig. 30) variously located; anteriormost pore often bilaterally paired; sternites sometimes deeply depressed in midline. Anal opercula of males unmodified, anal glands absent, tergite 9 not modified. Penis (Figs. 7, 8, 15, 16, 24–28, 43) distinctive, with four apical setae fused in pairs and their bases much thickened, movable fingers enlarged, middle pair of dorsal setae sometimes reduced or absent.

Key to Species

1a. Dorsum with a distinct color pattern of black and brown (Fig.1); males with 4 sternal pores ..... ***raveni***, n. sp.
1b. Dorsum uniformly colored ..... 2.
2a. Body length about 2.5 mm ..... 3.
2b. Body length about 2.0 mm, usually less ..... 4.
3a. Males with 4 sternal pores; penis (Fig.16) with 4 ventral setae, their bases contiguous . ***tillierorum***, n. sp.
3b. Males with 2 sternal pores; penis (Fig. 26) with 2 ventral setae, their bases widely separated ..... *aelleni* Juberthie.
4a. Body length about 1.75 mm; males with 2 sternal pores (a third pore present in a minority of specimens from one locale), sternites deeply depressed; penis (Fig. 24) with 1 ventral seta, median dorsal setae (Fig. 25) as large as other dorsal setae ..... ***juberthiei***, n. sp.
4b. Body length 2–2.15 mm; males with 3 sternal pores, sternites deeply depressed (Fig. 30) or not, penis with more than 1 ventral seta, median dorsal setae reduced in size or absent ..... 5.
5a. Male sternites deeply depressed (Fig. 30); penis (Fig. 28) with 6 dorsal setae, the median pair reduced ..... ***platnicki***, n. sp.
5b. Male sternites not depressed; penis (Fig. 43) with 4 dorsal setae, the median pair absent ... ***ninqua***, n. sp.

Troglosiro raveni, new species
Figs. 1–8

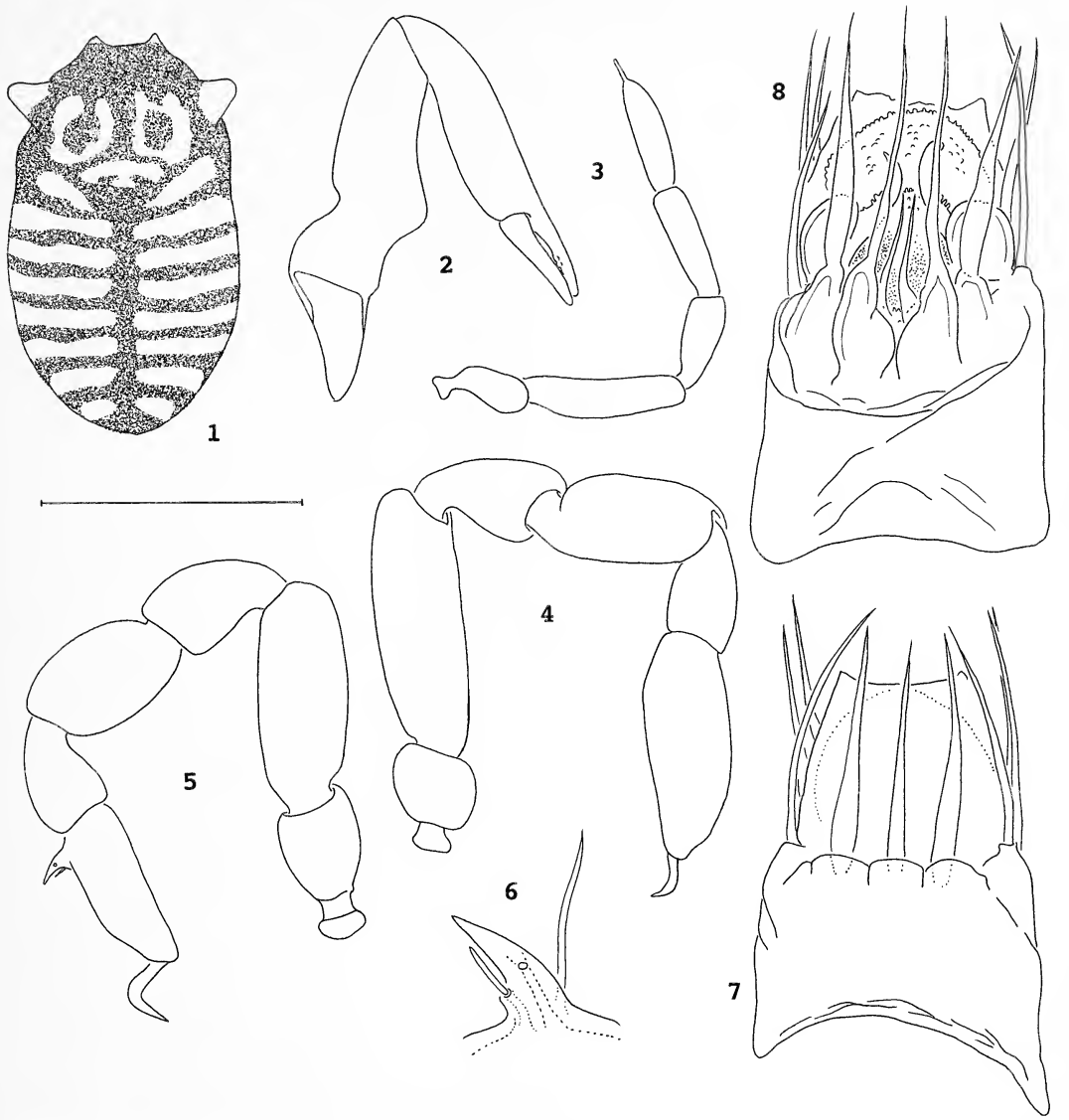
Type data.—Holotype male and paratype female (MNHN) from Berlese sample of dry forest litter, Col des Rousettes, 490 m elevation, New Caledonia, collected 29 May 1987 by Robert Raven and Norman Platnick.

Etymology.—The name honors one of the collectors, a noted Australian arachnologist.

Distribution.—Known only from the type locality.

Diagnosis.—Distinct from its congeners in the color pattern.

Description.—*Male:* Total length 2.03, width across ozophores 1.13, greatest width (gW) 1.2, L/gW = 1.69. Body (Fig. 1) generally egg-shaped, widest at posterior part of cephalothorax. Dorsum shining, with pebbled microsculpture. Ozophores close to cephalothorax margin, directed laterally. Cephalothoracic sulcus indistinct; abdominal sulci scarcely visible. Posterior end of body evenly rounded. Abdominal sternites with 4 gland pores in midline; anteriormost in posterior margin of sternite 2+3, appears as pair of pores at high magnification; following 3 pores single, at anterior margins of sternites 4, 5, 6. Pebbled ornamentation absent from sternal midline, sterna not depressed. First cheliceral segment (Fig. 2) 0.83 long, 0.19 wide, low dorsal crest present. Second cheliceral segment 0.71 long, 0.14 wide, straight, evenly tapered, fixed finger 0.23 long, 32% length of second cheliceral segment. Cheliceral teeth regular. Palpal segments (Fig. 3) 0.21, 0.33/0.08 (4.13), 0.22, 0.26/0.08 (3.25), 0.26. Legs robust, with heavily pebbled ornamentation. Leg 1 (Fig. 4) segments 0.55/0.19 (2.9), 0.34/0.17, 0.32/0.19 (1.68), 0.14/0.23, 0.49/0.18. Leg 4 (Fig. 5) segments 0.45/0.19 (2.37), 0.31/0.19, 0.32/0.21 (1.52), 0.26/0.16, 0.38/0.14. Adenostyle (Fig.6) slightly curved, acutely tri-

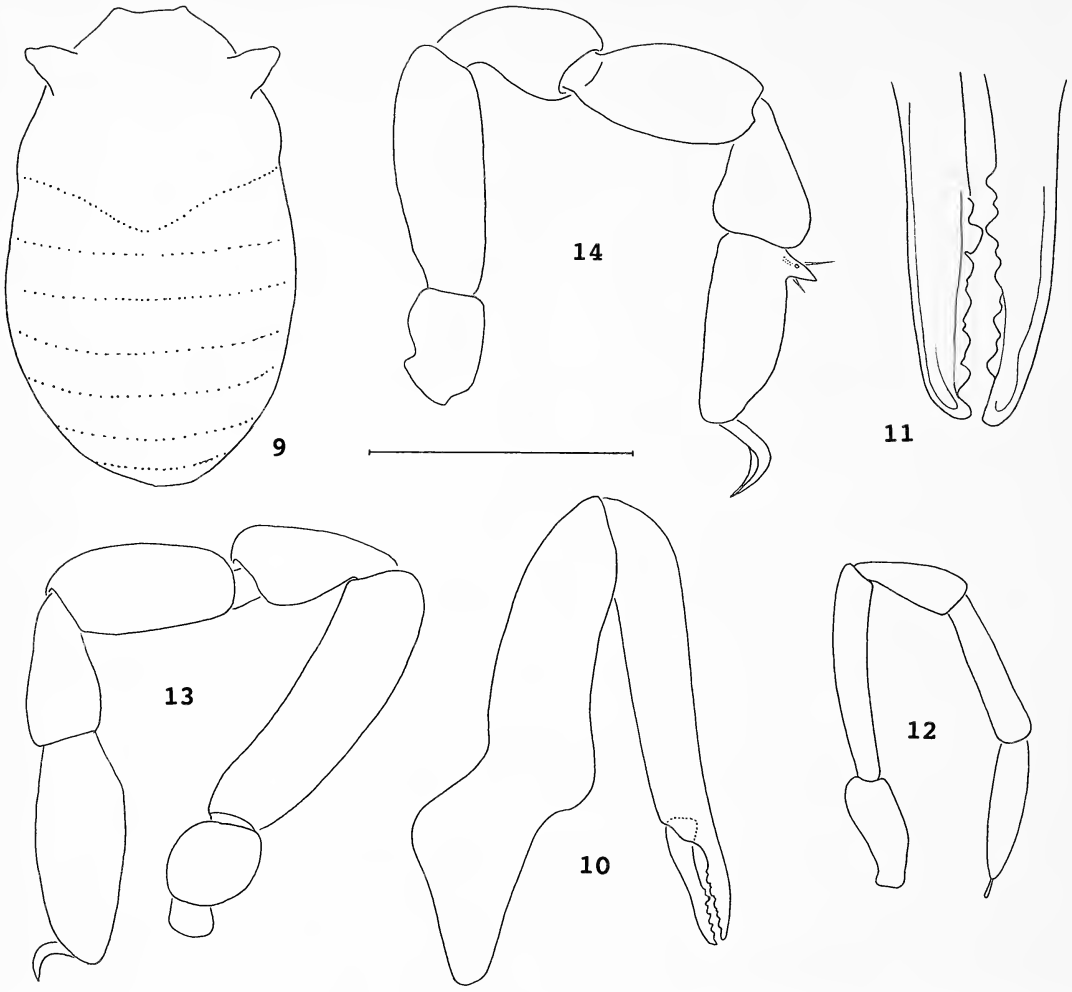


Figures 1–8.—***Troglosiro raveni***, new species, male: 1, dorsum; 2, chelicera; 3, pedipalp; 4, first leg; 5, fourth leg; 6, adenostyle; 7, penis, ventral view, tip of ventral plate broken off; 8, penis, dorsal view, tip of ventral plate broken off. Scale line: 1.5 mm for 1; 0.6 mm for 2–5; 0.3 mm for 6; 0.15 mm for 7, 8.

angular. Penis in ventral view (Fig.7) with three ventral setae; in dorsal view (Fig.8) with three lateral setae on each side and three pairs of dorsal setae, median dorsal setae much reduced, lateral two bladelike. Apical setae broken off in holotype (and only) male, probably typical for genus. Gonopore structures: ventral plate large, with toothed semicircular margin; movable fingers with very large basal lobes, fingers with toothed lateral margins; gonopore lip with fine teeth. Color pattern as illustated (Fig. 1).

Female: Total length, 2.00 mm. Closely resembling male in all nonsexual characters.

Remarks.—Though the characteristic large apical setae are broken off in the only male, they were clearly present at one time, and the other characters of this species argue for its inclusion in *Troglosiro*. Color patterns are rare in cyphophthalmids; usually the dorsum is evenly colored black to light yellowish tan, with differences in surface texture marking segmental limits. Often the legs are a lighter color than the dorsum, or



Figures 9–13.—***Troglosiro tillierorum***, new species, male: 9, dorsum; 10, chelicera; 11, cheliceral teeth; 12, pedipalp; 13, first leg; 14, fourth leg. Scale line: 1.5 mm for 9; 0.6 mm for 10, 12, 13, 14; 0.15 for 11.

have light-colored distal segments. Forster (1948), however, described several species of the New Zealand genus *Rakaia* Forster with distinctive color patterns not unlike that of *Troglosiro raveni*. All the known species of *Rakaia* lack sternal glands in the males and have very well-developed modifications of the anal plate and posterior tergites.

Troglosiro tillierorum, new species
Figs. 9-16

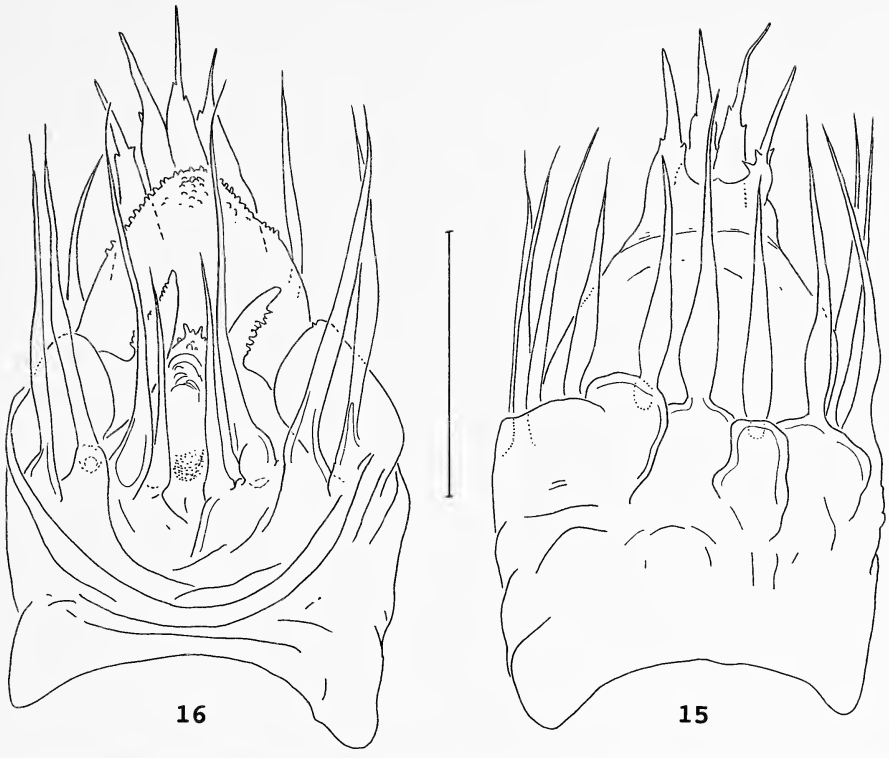
Type data.—Holotype male (MNHN) from Berlese sample from humid forest, Bobeitio (Tillier station 16a; 165°01′01″E, 20°57′13″S), 350 m elevation, New Caledonia, collected 17 November 1988 by A. and S. Tillier.

Etymology.—The name honors the collectors, diligent students of the New Caledonian fauna.

Distribution.—Known only from the type locality.

Diagnosis.—Closest in size and appendage proportions to *T. aelleni*, but with 4, rather than 2, ventral penial setae, and 4, rather than 2, sternal pores. Distinct from the other species of the genus in its larger size.

Description.—*Male:* Total length 2.5, width across ozophores 1.33, greatest width (gW) 1.33, L/gW = 1.88. Body (Fig. 9) generally egg-shaped, widest at posterior part of cephalothorax. Dorsum shining, with pebbled microsculpture. Ozophores close to cephalothorax margin, directed laterally, slightly constricted apically. Cephalothoracic sulcus distinct; abdominal sulci less so. Posterior end of body evenly rounded. Abdominal sternites with 4 gland pores in midline; anteriormost in posterior margin of sternite 2+3,



Figures 15, 16.—***Troglosiro tillierorum***, new species, male: 15, penis, ventral view; 16, penis, dorsal view. Scale line: 0.15 mm.

second near midlength of sternite 4, third near midlength of sternite 5, fourth in sulcus between sternites 6 and 7. Pebbled ornamentation absent from sternal midline, sterna not depressed. First cheliceral segment (Fig. 10) 1.08 long, 0.21 wide, dorsal crest absent. Second cheliceral segment 0.99 long, 0.13 wide, straight, evenly tapered, fixed finger 0.21 long, 21% length of second cheliceral segment. Cheliceral teeth (Fig. 11) somewhat irregular, perhaps due to wear. Palpal segments (Fig. 12) 0.26, 0.48/0.07 (6.8), 0.26, 0.32/0.07 (4.5), 0.30. Legs robust, with heavily pebbled ornamentation. Leg 1 (Fig. 13) segments 0.63/0.19 (3.1), 0.37/0.18, 0.40/0.19 (2.1), 0.32/0.17, 0.48/0.19. Leg 4 (Fig. 14) segments 0.53/0.19 (2.8), 0.37/0.20, 0.34/0.20 (1.7), 0.31/0.21, 0.41/0.17. Adenostyle not curved, acutely triangular. Penis in ventral view (Fig. 15) with 4 ventral setae; in dorsal view (Fig. 16) with 3 lateral setae on each side and 6 dorsal setae, median dorsal setae much reduced. Apical setae typical for genus. Gonopore structures: ventral plate large, with toothed semicircular margin; movable fingers with very large, laterally protruding basal lobes, fingers with toothed lateral margins; gonopore lip with small, blunt teeth.

Female: not collected.

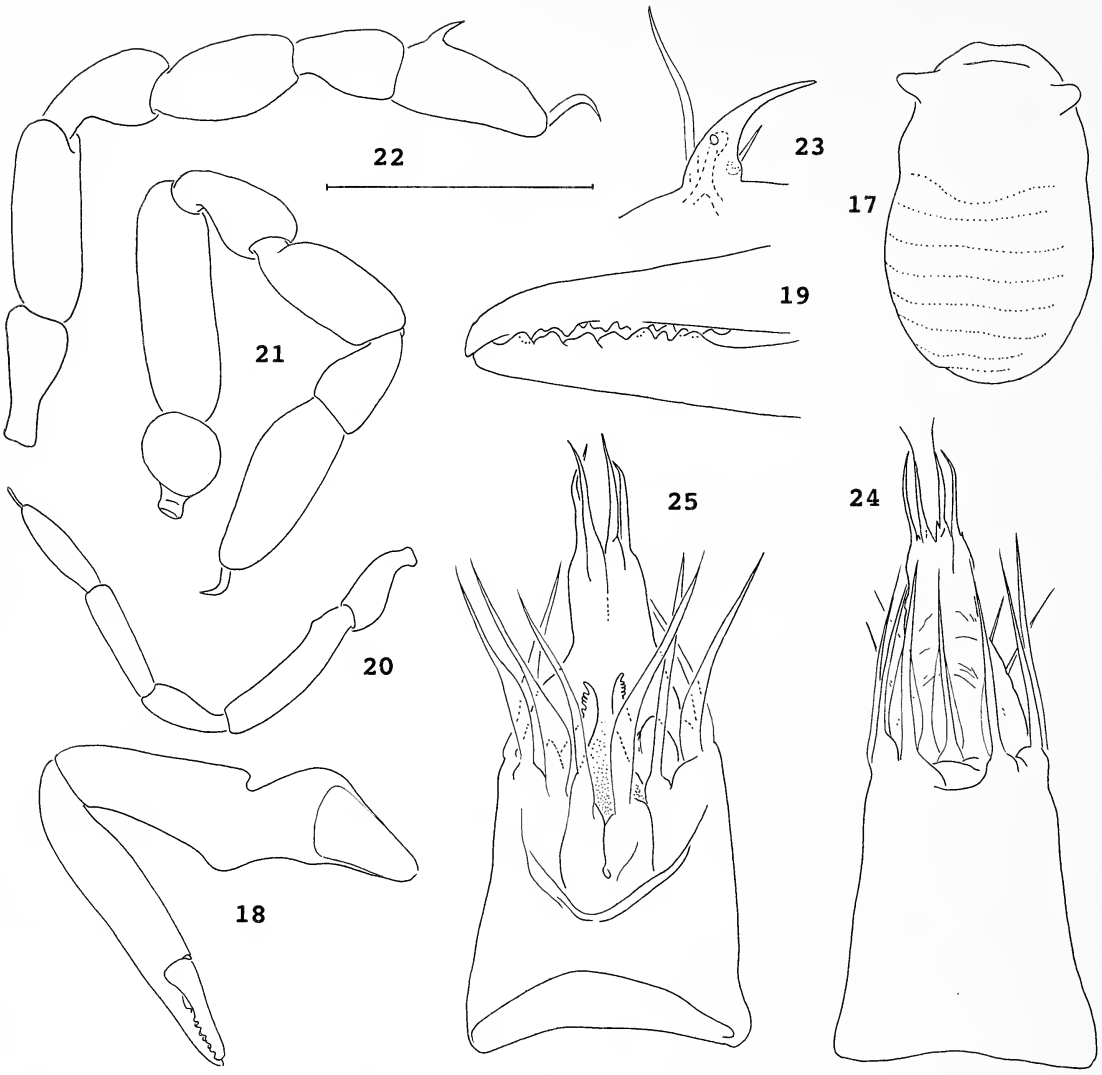
Remarks.—This species is nearly identical in size and appendage measurements to the type specimen of *T. aelleni*, but the penis and the sternal pores are quite different. With only the single male of *T. tillierorum* available, and only two males of *T. aelleni* known, it is difficult to assess the range of variation in either population. However, previous experience in other genera suggests that differences of this magnitude constitute species distinctions.

Troglosiro aelleni Juberthie
Fig. 26

Troglosiro aelleni Juberthie, 1979:222 (male holotype and male paratype from Grotte d'Adio (Ninrin-Reu), near Poya, Mt. Adio, 200 m altitude, collected by Aellen and Strinati, 2 April 1977; in Muséum d'Histoire naturelle de Genève, Switzerland, examined).

I examined the holotype slides and specimens and found Juberthie's 1979 description entirely accurate. Juberthie did not illustrate a ventral view of the penis, supplied here as Fig. 26. There are 2 ventral setae.

Surprisingly, no additional specimens of this species turned up in the Tillier and Platnick-



Figures 17–25.—***Troglosiro juberthiei***, new species, male: 17, dorsum; 18, chelicera; 19, cheliceral teeth; 20, pedipalp; 21, first leg; 22, fourth leg; 23, adenostyle; 24, penis, ventral view; 25, penis, dorsal view. Scale line: 1.5 mm for 17; 0.6 mm for 18, 20-22; 0.3 mm for 23; 0.15 mm for 19, 14, 25.

Raven collections. It is possible that the species is limited to the cave at the type locality.

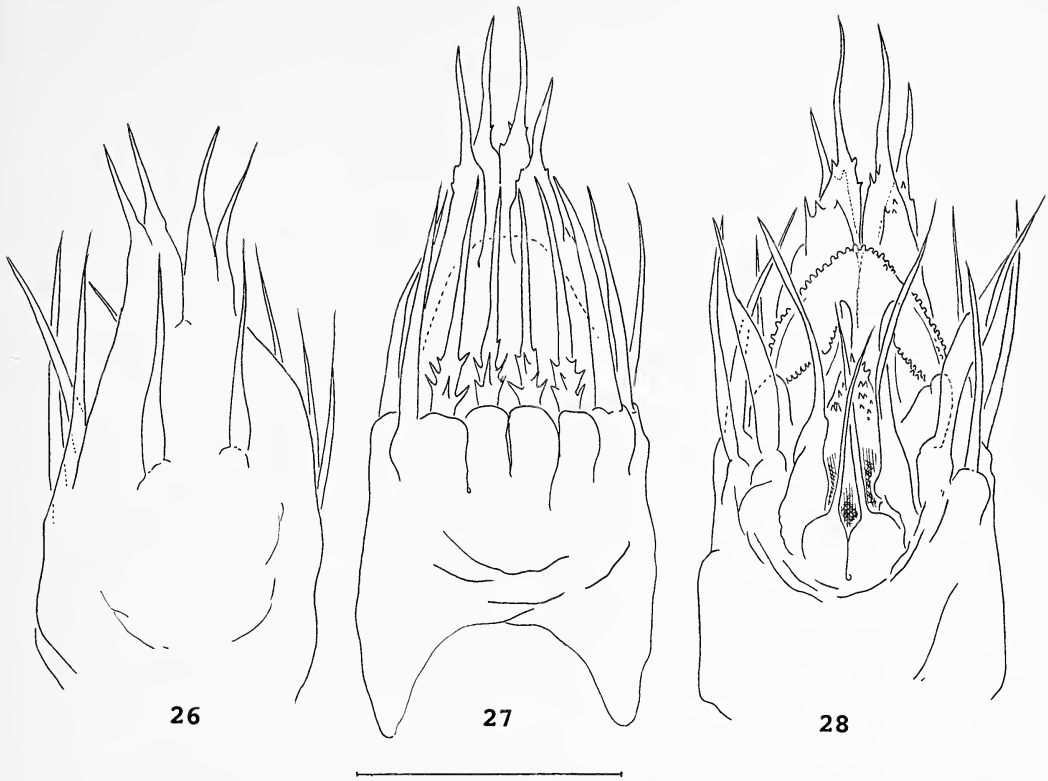
Troglosiro juberthiei, new species
Figs. 17–25

Type data.—Holotype male, paratype female (MNHN) and six additional male and one additonal female paratypes (AMNH) from Berlese sample of montane forest litter, Riviere Bleue, 280 m elevation, collected 21 May 1987, by N. I. Platnick and R. J. Raven.

Etymology.—The name honors Dr. C. Juberthie, Laboratoire souterrain du C. N. R. S., Moulis, St. Girons, France, who described the genus *Troglosiro*, and who has contributed more than anyone else to our understanding of cyphophthalmid Opiliones.

Distribution.—In addition to the type locality: NEW CALEDONIA: Plot VI I, Station 250 d, Riviere Bleue (166°39′16″E, 22°06′13″S), moist forest Berlese, 4 December 1986, A. and S. Tillier, 1 male.

Diagnosis.—Closest in size and appendage proportions to *T. platnicki* and *T. ninqua*, but with 1, rather than 3 or 4, ventral penial setae, and usually with 2, rather than 3, sternal pores. The median dorsal penial setae are of normal



Figures 26–28.—Penes.–26, *Troglosiro aelleni* Juberthie, ventral view; 27, 28, ***Troglosiro platnicki***, new species: 27, ventral view; 28, dorsal view. Scale line: 0.15 mm.

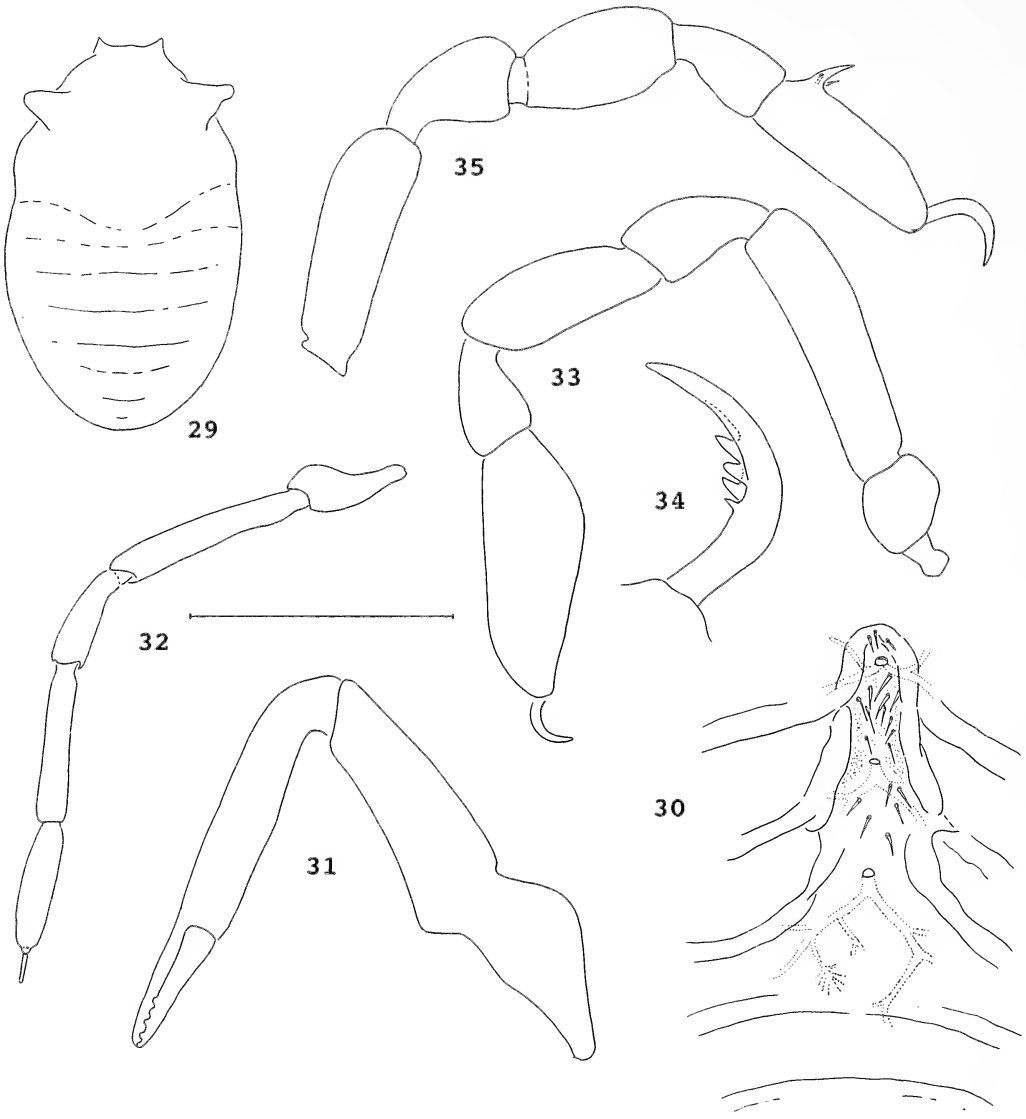
size, rather than reduced. Distinct from the other species of the genus in its smaller size.

Description.—*Male:* Total length 1.77, width across ozophores 1.00, greatest width (gW) 1.10, L/gW = 1.61. Body (Fig. 17) generally egg-shaped, widest at posterior part of cephalothorax. Dorsum shining, with pebbled microsculpture. Ozophores close to cephalothorax margin, directed laterally, slightly constricted apically. Cephalothoracic sulcus rather indistinct; abdominal sulci even less so. Posterior end of body evenly rounded. Abdominal sternites with 2 gland pores in midline; anteriormost in posterior margin of sternite 2+3, second near midlength of sternite 4; in two of seven males from the type series a third near midlength of sternite 5. Pebbled ornamentation absent from sternal midline, sterna 4 and 5 depressed. First cheliceral segment (Fig. 18) 0.82 long, 0.18 wide, with pronounced dorsal crest. Second cheliceral segment 0.75 long, 0.12 wide, straight, scarcely tapered, fixed finger 0.24 long, 32% length of second cheliceral segment. Cheliceral teeth (Fig. 19) irregular. Palpal segments (Fig. 20) 0.22, 0.36/0.07 (5.14), 0.19, 0.25/0.06 (4.2), 0.23. Legs robust, with heavily pebbled ornamentation. Leg 1 (Fig. 21) segments 0.50/0.16 (3.1), 0.28/0.15, 0.30/0.15 (2.0), 0.24/0.13, 0.40/0.17. Leg 4 (Fig. 22) segments 0.40/0.15 (2.7), 0.29/0.17, 0.28/0.17 (1.65), 0.23/0.15, 0.34/0.15. Adenostyle (Fig. 23) curved, acuminate. Penis in ventral view (Fig. 24) with 1 ventral setae, 3 lateral setae on each side; in dorsal view (Fig. 25) with 6 dorsal setae, median dorsal setae not reduced. Apical setae somewhat more gracile than typical for genus. Gonopore structures: ventral plate large, with toothed semicircular margin; movable fingers with very large, laterally protruding basal lobes, fingers with toothed lateral margins; gonopore lip with small, blunt teeth.

Female: Slightly larger (length of paratype 1.83), otherwise similar to male in nonsexual characters.

Troglosiro platnicki, new species
Figs. 27–35

Type data.—Holotype male (MNHN) from Berlese sample from humid forest, Riviere Bleue



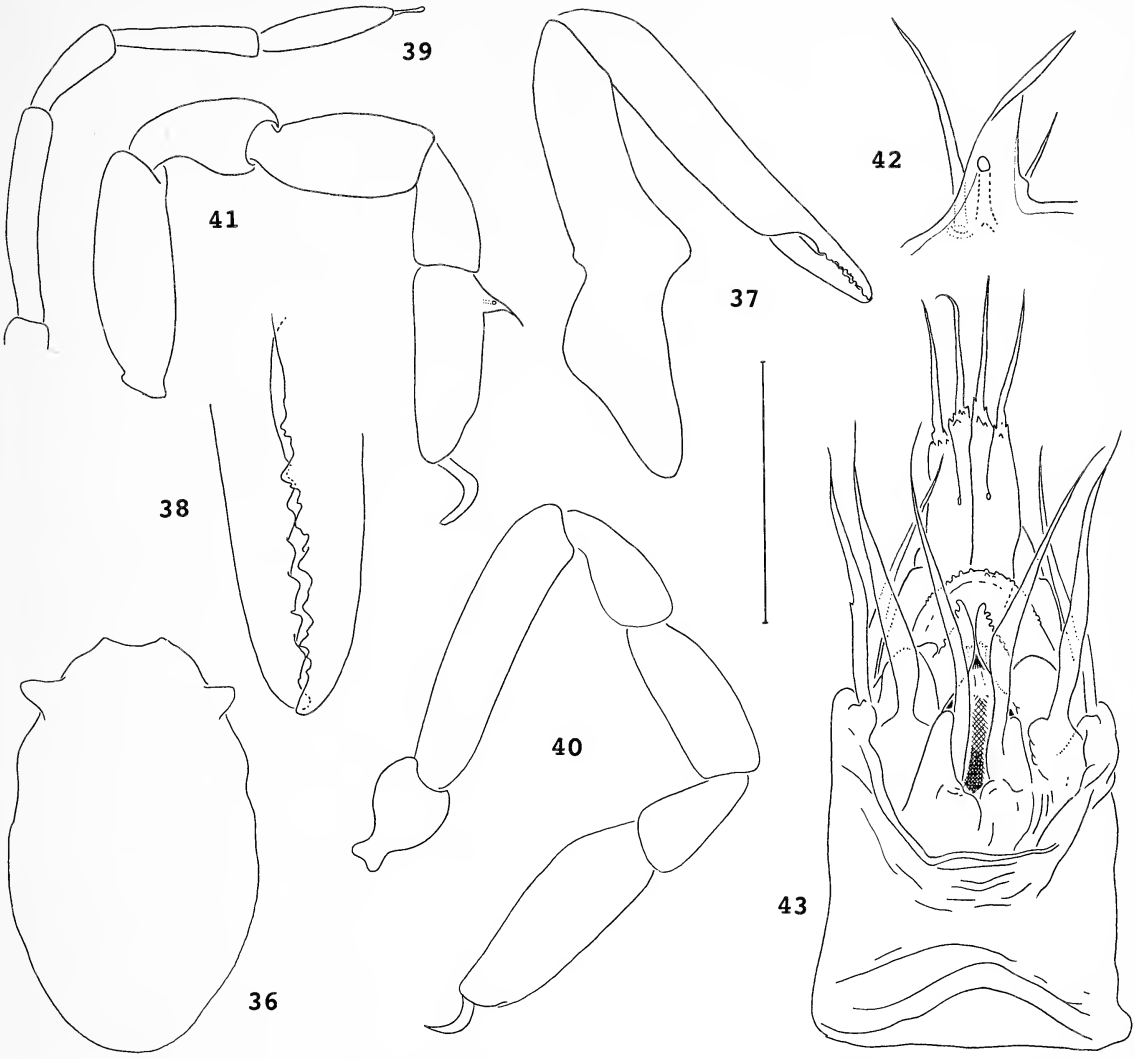
Figures 29–35.—***Troglosiro platnicki***, new species, male: 29, dorsum; 30, ventral view of anterior abdominal segments; 31, chelicera; 32, pedipalp; 33, first leg; 34, claw of second leg; 35, fourth leg. Scale line: 1.5 mm for 29; 0.75 mm for 30; 0.6 mm for 31–33, 35; 0.15 mm for 34.

(Tillier station 250k, plot VI X; 166°39′16″E, 22°06′13″S), 160 m elevation, New Caledonia, collected 7 July 1987 by A. Tillier.

Etymology.—The name honors Dr. Norman I. Platnick, internationally known authority on arachnids.

Distribution.—In addition to the type locality, NEW CALEDONIA: from the following Berlese samples of moist forest litter along Riviere Bleue, same coordinates and altitude as type collection. Tillier Sta. 250c, plot VI 0, A. & S. Tillier, 3 November 1986, 2 males, female (MNHN); Sta. 250h, plot VI 0, A. & S. Tillier, 6 April 1987, 4 males, 2 females (MNHN). Riviere Bleue, Berlese sample from humid forest (Tillier station 251d, plot VII 0; 166°40′01″E, 22°05′59″S), 170 m elevation, A. & S. Tillier, 11 December 1986, male, female (MNHN); wet forest along Riviere Bleue, 280 m elevation, N. Platnick & R. Raven, 21 May 1987, male (AMNH); Berlese of rainforest litter, Mt. Dzumac, N. Platnick & R. Raven, 28 May 1987, male (AMNH).

Diagnosis.—Distinct from others species in having 4 ventral setae on the penis, with their



Figures 36–43.—***Troglosiro ninqua***, new species, male: 36, dorsum; 37, chelicera; 38, cheliceral teeth; 39, pedipalp; 40, first leg; 41, fourth leg; 42, adeonstyle; 43, penis, dorsal view. Scale line: 1.5 mm for 36; 0.6 mm for 37, 39–41; 0.3 mm for 42; 0.15 mm for 38, 43.

bases strongly toothed (Fig. 27); the sterna of males are deeply depressed, the depression with pronounced lateral rims (Fig. 30).

Description.—*Male:* Total length 2.0, width across ozophores 1.08, greatest width (gW) 1.23, L/gW = 1.63. Body (Fig. 29) generally egg-shaped, widest at posterior part of cephalothorax. Dorsum shining, with pebbled microsculpture. Ozophores close to cephalothorax margin, directed laterally, slightly constricted apically. Cephalothoracic sulcus indistinct; abdominal sulci less so. Posterior end of body evenly rounded. Abdominal sternites with 3 gland pores in midlines of sternites 2, 3, and 4 (Fig. 30); these sternites deeply depressed, with few scattered setae, depression with distinct lateral rims. First cheliceral segment (Fig. 31) 0.97 long, 0.19 wide, dorsal crest very low. Second cheliceral segment 0.92 long, 0.13 wide, straight, scarcely tapered, fixed finger 0.30 long, 33% length of second cheliceral segment; cheliceral teeth regular. Palpal segments (Fig. 32) 0.23, 0.43/0.075 (6.14), 0.23, 0.33/0.06 (5.5), 0.29. Legs robust, with heavily pebbled ornamentation. Leg 1 (Fig. 33) segments 0.60/0.15 (4.0), 0.32/0.16, 0.39/0.16 (2.4), 0.24/0.14, 0.55/0.21. Leg 4 (Fig. 35) segments 0.52/0.16 (3.3), 0.32/0.19, 0.33/0.20 (1.7), 0.26/0.13, 0.43/0.15. Adenostyle slightly curved, acutely

triangular. Penis in ventral view (Fig. 27) with 4 ventral setae, each toothed at base; in dorsal view (Fig. 28) with 3 lateral setae on each side and 6 dorsal setae, median dorsal setae much reduced. Apical setae typical for genus, but with more coarse teeth basally. Gonopore structures: ventral plate large, with toothed semicircular margin; movable fingers with very large, laterally protruding basal lobes, fingers with lateral margins bearing small rounded teeth; gonopore lip with small, acute teeth.

Females: Somewhat larger (paratype 2.14 long), similar to males in nonsexual characters.

Remarks.—This species is nearly identical in size and appendage measurements to *T. ninqua*, but the toothed ventral setae of the penis and the deeply depressed male sterna of the present species distinguish the two.

Troglosiro ninqua, new species
Figs. 36-43

Type data.—Holotype male and female paratype (MNHN) from Berlese sample from humid forest, Mt. Ninqua (Tillier station 288, 166°09′03″E, 21°44′24″S), 1000 m elevation, New Caledonia, collected 28 October 1986 by A. and S. Tillier.

Etymology.—The name, a noun in apposition, is after the type locality.

Distribution.—Known only from the type locality.

Diagnosis.—Closely related to *T. platnicki*, but differing in lacking median dorsal setae of the penis, and having smooth, not toothed, ventral setae; the sterna of males are only slightly depressed rather than having a deep, rimmed depression as in *T. platnicki*.

Description.—*Male:* Total length 2.12, width across ozophores 1.13, greatest width (gW) 1.3, L/gW = 1.6. Body (Fig. 36) generally egg-shaped, widest at posterior part of cephalothorax. Dorsum shining, with pebbled microsculpture. Ozophores close to cephalothorax margin, directed laterally, slightly constricted apically. Cephalothoracic and abdominal sulci nearly obsolete. Posterior end of body evenly rounded. Abdominal sternites with 3 gland pores in midlines of sternites 2, 3, and 4; these sternites slightly depressed, lacking usual pebbled microsculpture. First cheliceral segment (Fig. 37) 1.02 long, 0.19 wide, dorsal crest very low. Second cheliceral segment 0.91 long, 0.14 wide, straight, scarcely tapered, fixed finger 0.23 long, 25% length of second cheliceral segment; cheliceral teeth complex but regular, each consisting of a main blade and two smaller points (Fig. 38). Palpal segments (Fig. 39) 0.23, 0.46/0.08 (6.13), 0.24, 0.31/0.05 (6.2), 0.33. Legs robust, with heavily pebbled ornamentation. Leg 1 (Fig. 40) segments 0.66/0.14 (4.71), 0.32/0.15, 0.41/0.16 (2.6), 0.29/0.14, 0.50/0.19. Leg 4 (Fig. 41) segments 0.50/0.17 (2.9), 0.26/0.17, 0.38/0.18 (2.1), 0.29/0.14, 0.42/0.15. Adenostyle (Fig. 42) slightly curved, acutely triangular. Penis in ventral view with 4 ventral setae, basally bladelike, set on raised sockets; in dorsal view (Fig. 43) with 2 lateral setae on each side and 4 dorsal setae, median dorsal setae absent. Apical setae typical for genus, bases somewhat more elongate, smoother. Gonopore structures: ventral plate large, with vaguely toothed semicircular margin; movable fingers with moderate, laterally protruding basal lobes, fingers with lateral margins bearing small rounded teeth; gonopore lip narrow, with small, acute teeth.

Female: Somewhat larger (paratype 2.13 long), similar to males in nonsexual characters.

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THE INFLUENCE OF PREY AVAILABILITY AND HABITAT ON ACTIVITY PATTERNS AND ABUNDANCE OF *ARGIOPE KEYSERLINGI* (ARANEAE: ARANEIDAE)

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ABSTRACT. I examined habitat relationships and prey abundance to determine which (if either) of these factors was more important in determining the local density patterns of the Saint Andrew's Cross spider, *Argiope keyserlingi* Karsch. Focusing on the relationship between a predator and its prey distribution presupposes that prey capture rate is crucial to the biology of the predator. I also studied the influence of prey capture on survival, reproduction and behavior of *A. keyserlingi* as a test of this assumption. Reproduction of females was influenced by food availability under laboratory conditions. Survival was higher among individual females provided with supplemental food in a field experiment. Adult female *A. keyserlingi* moved less frequently when they were provided with supplemental food. Features of vegetation were correlated with patterns of spatial distribution of this spider. There was a highly significant correlation between spider density on the study plots and the density of the understory shrubs that were favored as web sites. On a broad scale, seasonal phenology of activity in *A. keyserlingi* was positively correlated with potential prey abundance. At the scale of individual study plots, there is evidence that prey distribution was unpredictable in both time and space and that neither the activity patterns nor local density of *Argiope keyserlingi* tracked these fluctuations.

Recent experimental studies of arachnid ecology have examined the influence of prey availability and the presence of competitors on the distribution and abundance of these predators (Wise 1979; Greenstone 1978; Schaefer 1978; Horton & Wise 1983; Janetos 1983; Rypstra 1983; Riechert & Cady 1983; Spiller 1984, 1986; Miyashita 1986; Bradley 1989). Of these studies the experimental work of Spiller (1984) provides the only direct evidence of exploitation competition acting on unrestrained spiders in the field.

Riechert & Cady (1983) suggest that interference and intraspecific exploitation competition are more important than interspecific exploitation competition among spiders. For a variety of arachnids interference competition and/or cannibalism influences the number and distribution of individuals (Riechert 1974; Turner & Polis 1979; Riechert & Cady 1983; Wise 1983, 1984; Polis & McCormick 1986a, 1986b; Rubenstein 1987). Despite the paucity of evidence for exploitation competition, several studies have shown that individual arachnids experience shortages of food that limit reproduction (Wise 1975, 1979; Gillespie & Caraco 1987; Morse & Fritz 1982; Fritz & Morse 1985; Suter 1985). These apparently contradictory results may be reconciled if there is no clear density-dependent relationship between arachnids and their prey (Riechert & Lockley 1984). This situation has also been demonstrated in the predatory beetle *Hyphydrus ovatus* L. (Juliano & Lawton 1990).

Wise (1984) suggests that food-limitation does not necessarily imply competition when resources can neither be predicted nor dominated. This situation is possible because individual spiders may encounter insufficient numbers of prey even though prey populations are not regulated by spider density. In contrast, two studies of agroecosystems indicate that spiders do regulate prey populations in these relatively simple environments (Oraze & Gigarick 1989, Riechert & Bishop 1990).

Most arachnids are generalist predators and because prey populations vary unpredictably in both space and time, the foraging success of an individual spider may have little impact on its neighbors. Spiders which capture insufficient prey suffer a "relative shortage of food" (Andrewartha & Birch 1954). Relative shortage occurs when some individuals do not obtain sufficient food yet food is available in the environment. This is often the result of the inability of the predator to locate food, rather than its absence (Andrewartha & Birch 1984). Because polyphagous spi-

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ders probably do not regulate populations of their prey and live among many other insectivores, Andrewartha & Birch (1984, p. 49) would refer to this situation as a case of extrinsic relative food shortage. Relationships in which the prey (donor) controls predator (recipient) density but not the reverse are referred to as donor-controlled systems (Pimm 1982). I will examine this idea in the context of the omnivorous predator *Argiope keyserlingi*.

It has been shown that habitat structure strongly influences distribution and abundance of orb-web building spiders (Colebourn 1974; Schaefer 1978; Rypstra 1983, 1986) and other arachnids (Riechert 1977, 1979, 1981; Bradley 1986). There is some evidence that suitable foraging or retreat sites may even limit population density and determine the pattern of dispersion of individuals among ground foraging spiders (Riechert 1976) and scorpions (Bradley 1986). Riechert & Gillespie (1986) provided a summary table of the evidence for habitat choice by spiders which indicated that both vegetation structure and prey were important factors, but that very few studies compared these factors. Janetos (1986) suggested that prey encounter rates have a direct impact on web-site occupancy because spiders abandon unproductive sites but also stated that variability of prey encounter at a particular site had been little studied.

The question thus arises, are spider abundance and activity responsive to prey variability, to habitat characteristics, or to some combination of both factors? I examined this question in an empirical study of temporal and spatial relationships between a generalist predator, the orb-weaving spider *Argiope keyserlingi* Karsch, and its habitat and arthropod prey. My study had two primary goals: 1) to assess the importance of variation in prey availability on activity patterns of *A. keyserlingi* and 2) to compare the relative influence of prey abundance and habitat features on the pattern of local distribution of *A. keyserlingi* individuals. A central assumption of community ecology has been that the abundance of food resources is crucial in determining patterns of predator distribution and abundance (Wiens 1989, p. 16). In this study I tested the assumption that food availability is important to *A. keyserlingi* by assessing the influence of foraging success on survival and reproduction in female *A. keyserlingi*.

Argiope keyserlingi is common in a variety of habitats along the east coast of Australia from NE Queensland south to NE Victoria. In Australia this spider is commonly but incorrectly known as *A. aetheria* (Levi 1983). It builds orb webs in low vegetation in open habitats, including heathland and salt marsh, as well as the understory of evergreen sclerophyl woodlands and forests. In the Hawkesbury Sandstone plateau of New South Wales they seem most abundant in the understory of dry open forest (Benson & Fallding 1981). This study focused on one open forest population of this species. After emergence from the egg case, second-instar *A. keyserlingi* disperse (often by ballooning). Fresh egg cases collected in the field and kept in the laboratory hatched 14–25 days after they were laid ($\bar{x}$ = 19, SEM = 1.4, n = 9). Juveniles build their first webs in late summer (February and March). They over-winter as immatures and emerge in spring (November). Data from spider censuses on the study area indicate a brief synchronous activity period (Fig. 1A). In addition to these census data, qualitative observations for the previous (1983/84) and subsequent (1986/87) summers conform to the same restricted activity period. Individuals found in other habitats of the Sydney region are active for much longer periods during the year. Adult female *A. keyserlingi* usually die after laying eggs, and I often found their carcasses hanging in or lying on the ground below the web in January and February. A few *A. keyserlingi* females survive the winter and become active again during the following spring. These females may either represent late-maturing or truly biennial individuals.

METHODS

General methods.—The study site was located in Brisbane Water National Park, near the University of Sydney's Crommelin Biological Research Station at Pearl Beach NSW (33° 33′ S, 151° 18′ E). The habitat is dominated by *Casuarina torulosa* Ait. (70% of trees), *Angophora costata* (Gaertn.) J. Britt, *Eucalyptus* spp. and *Syncarpia glomulifera* (Sm.) Niedenzu. The understory is relatively open, with many shrubs, principally *Xanthorrhoea resinosa* Pers., *Dodonaea triquetra* Wendl., *Livistona australis* (R. Br.) Mart., and *Lasiopetalum ferrugineum* Sm. The site is on a north-facing hillside with a few exposed rock outcrops and a dense mat of *Casuarina* litter (5–20 cm deep). Sixteen 0.023 ha (15 m × 15 m) square sampling plots were established and marked with wooden stakes. The plots were separated by a minimum of 5 m.

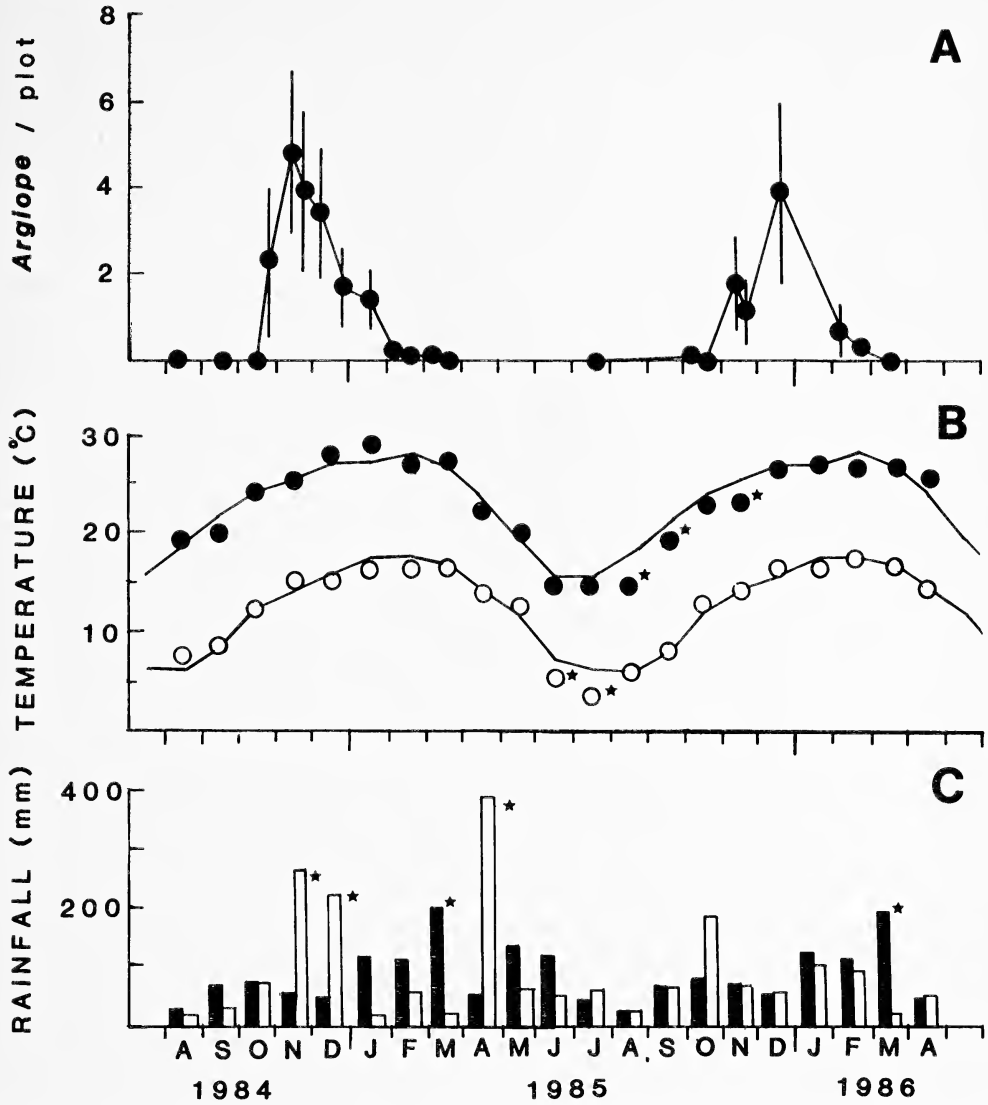

Figure 1.—Activity phenology and weather statistics for *Argiope keyserlingi* during the 1984/85 and 1985/86 seasons. **A.** *Argiope* activity in mean number of spiders per plot ($n = 16$) for each sampling date. The vertical bars indicate the 95% confidence limits on this mean. **B.** Mean monthly temperature at the study area (°C). The solid dots are the mean high temperatures for the sampling month, and the open dots are the mean low temperatures for the sampling month. The lines connect the normal mean high temperature and normal mean low temperature patterns based on the previous 10 years of weather records ($n = 3647$ sample dates). Stars indicate monthly averages that differ from the 10-year average (z-test, $P < 0.05$). **C.** Monthly rainfall in mm, the solid bars are means based on the previous 10 years of weather records, the open bars are the actual rainfall totals for the sampling month. Stars indicate rainfall values that differ from the 10-year average (z-test, $P < 0.05$).

The number, DBH (diameter at breast height) and identity of all trees and the number of perennial shrubs were counted for each study plot. Twelve summary habitat variables (Table 1) were subjected to principal components analysis. The principal component scores for each plot along the first three axes were compared to measures of spider density using the Pearson product-moment correlation (r_p). Mean elevation was calculated for each plot. Features of the perennial vegetation changed little during this study and were measured only once (spring 1986). Three descriptive variables (top thread length, sticky orb diameter, and height above ground at orb

Table 1.—*Argiope keyserlingi* density and habitat features on the 16 study plots. Variables: *Argiope* = $\bar{x}$ no. spiders/plot, Ang# = no. of *Angophora costata* and *A. floribunda,* Euc# = no. of trees in genus *Eucalyptus* (8 species), Cas# = no. of *Casuarina torulosa,* Bank# = no. of *Banksia serrata,* Syn# = no. of *Syncarpia glomulifera,* Totlg = total no. of trees, Diam = $\bar{x}$ diameter of trees (breast height), Totar = cross-sectional area of trees at breast height (m^2), Xanth = no. of *Xanthorrhoea resinosa,* Macz = no. of *Macrozamia communis,* Palm = no. of *Livistona australis,* Totsm = total no. of small shrubs, Totvg = Totlg + Totsm, Elev = $\bar{x}$ elevation of plot (m).

Plot	*Argiope* numbers ($\bar{x}$ spiders/plot)		Habitat features													
			Trees & large shrubs								Small shrubs					
#	84/85	85/86	Ang-#	Euc-#	Cas-#	Bank-#	Syn-#	Totlg	Diam	Totar	Xanth	Macz	Palm	Totsm	Totvg	Elev
1	7.5	3.7	0	2	11	9	0	22	18.2	0.85	7	3	31	41	63	35.1
2	10.8	8.3	0	3	32	0	0	35	19.0	1.61	25	4	30	59	94	35.1
3	4.0	0.3	1	1	24	3	0	30	17.0	1.13	2	0	24	26	56	36.3
4	4.0	5.0	2	2	26	3	0	32	15.6	1.47	6	2	9	17	49	36.3
5	4.3	3.7	1	7	3	5	0	11	21.0	1.37	4	1	6	11	22	37.5
6	2.3	1.3	6	0	5	2	0	21	12.1	0.31	3	0	0	3	24	37.5
7	1.0	0.0	0	8	29	1	2	32	11.0	0.40	3	0	1	4	36	41.5
8	1.5	2.0	0	3	12	2	7	29	16.7	0.95	1	0	0	1	30	37.5
9	1.5	2.0	0	4	24	0	0	27	18.8	1.03	0	0	17	17	44	37.5
10	2.0	0.7	0	4	37	1	5	47	14.0	1.03	0	1	4	5	52	37.8
11	2.3	1.3	0	0	35	0	3	38	13.7	0.68	2	0	2	4	42	38.7
12	5.3	1.7	0	6	41	0	5	52	13.8	1.04	4	1	6	11	63	37.5
13	3.0	1.7	1	2	27	1	9	40	15.3	1.39	0	7	46	53	93	37.2
14	3.3	1.7	2	8	15	3	8	36	14.3	0.81	1	4	9	14	50	36.9
15	1.0	0.3	1	17	14	0	0	32	13.8	0.67	0	0	1	1	27	38.4
16	1.5	2.0	0	4	21	1	0	26	13.2	0.47	0	2	13	15	47	36.3

center) were measured on 118 webs of *A. keyserlingi* mature females and 57 webs of immature females (total body length [tbl] < 7 mm). Total body length [tbl] was measured from the anterior end of the median ocular area to the tip of the opisthosoma. Mature male *Argiope keyserlingi* often inhabit the webs of females, and may act as kleptoparasites as they do in other species (Robinson & Robinson 1978; Suter 1985). Occasionally males are found in small webs alone; 15 such webs were measured and attributed to males. A sample of 26 *A. keyserlingi* egg cases was collected from areas adjacent to the main study area during early February 1985. These cases were weighed to the nearest 0.1 mg (Mettler balance), dissected and the number of eggs counted. A second sample of 19 egg cases collected in late February 1985 was weighed and maintained in the laboratory until the spiderlings emerged, and these were counted.

Spider censuses.—Visual censuses were conducted early in the morning on each of 14 dates between August and March 1984/85 and 9 dates between July and March 1985/86. Each plot was censused by walking slowly and looking in and under vegetation to detect *Argiope* webs. Repeat censuses were conducted by a second observer for the first two dates to verify the efficacy of the method. Each spider found was classified into one of 3 length categories (0–5 mm tbl, >5–7 mm tbl, >7 mm tbl).

Prey abundance.—Potential prey abundance was assessed using sticky-boards. Brown Masonite© boards 25.5 cm × 30.0 cm were placed on wood posts with the center of the board 1.2 m above the ground surface. The size of a sticky-board is similar to that of an adult *Argiope* web. Prey samples were collected once per month for each month when spiders were active (September—February). The sample for October 1985 was lost. On each sampling date a clear tight-fitting plastic bag was slipped over the board and both sides of the bag were coated with Tanglefoot© insect trapping adhesive. The plastic bag covered with Tanglefoot reflected the colors of the surrounding vegetation. Four boards were used on each of the 16 plots, with two oriented in a N–S direction and two oriented in an E–W

direction. On each sampling date the bags were left out for 24 h. To collect the bags, a larger plastic bag was inverted over the sticky-bag and both were removed. This left a clear plastic coating over the specimens, and all subsequent identifications and measurements were made through the plastic. These traps were used because they were successful in pre-sampling tests at capturing examples of the known prey items in the diet of *Argiope keyserlingi* (see below). Because sticky traps do not behave like spiders (Robinson & Robinson 1973; Rypstra 1982; Castillo & Eberhard 1983), I treated these data as an index of prey abundance rather than a measure of actual prey availability.

Each arthropod captured on the sticky-boards was measured to the nearest 1 mm (body length). Dry-weight biomass was estimated using regression equations appropriate for each taxon (Rogers et al. 1976, 1977). In cases where no appropriate regression equation was available, I calculated one from specimens captured in the study area. Any arthropods that were captured on the sticky traps which were not taken by *Argiope keyserlingi* when fed to spiders in the laboratory were eliminated from the sample. Most insects were identified to the ordinal level; large insects (> 10 mm body length) were identified to the family level. Three summary variables were tabulated for each sample of potential prey; 1) total number (NUMB), 2) number of large prey [> 5 mm body length, NBIGS], and 3) total biomass (BIOM). Analysis of spatial and temporal patterns of these potential prey variables were analyzed using a randomization test (Sokal & Rohlf 1981). A randomization test (repeated-measures ANOVA) was used because these data violated assumptions of traditional ANOVA (normality, heteroscedasticity) even after transformation. The randomization test (F-ratio used as test statistic) provided a robust, ANOVA-based way to examine variation among dates and across plots. A model that incorporated the repeated measures (boards on plots, dates) was used in the randomization-ANOVA. The SAS GLM (SAS 1988) procedure was used to calculate the SSQ values. A SAS data statement procedure was written to conduct the random re-assignments. Actual values were compared to 1000 randomized trials for estimation of significance. Parametric ANOVA (SAS GLM) was applied to web-characteristic data because these data met requisite assumptions. Correlation analyses were conducted to compare both temporal and spatial variation in the prey variables to spider census data. All data were tested for normality using the SAS univariate procedure. Pearson's product–moment correlation coefficient (r_p) was used when data met parametric assumptions. Spearman Rank correlation (R_s) was applied where data were not normally distributed. Autocorrelation with a lag of 1 was used to assess temporal variation in the spatial patterns of prey distribution. For this test the data for all four sticky boards were combined to produce one mean value of each prey variable for each date/plot combination.

Prey captured by *A. keyserlingi* in the field were also identified and measured. The frequency distribution of insects taken from *Argiope* webs was compared to that collected on the sticky-boards for both size and taxonomic grouping using a χ^2 goodness-of-fit test.

Stepwise multiple regression.—I compared the relative importance of vegetation and prey as independent variables for their ability to explain variation in *A. keyserlingi* density. The mean values of six habitat variables (number of *Xanthorrhoea,* number of *Macrozamia,* number of *Livistona,* number of large shrubs, plot elevation and the first Principal Component Score for each plot) and mean values of three prey variables from the sticky board sampling (NUMB, BIOM, NBIGS) were compared to the dependent variable *A. keyserlingi* density across the 16 sampling plots. The analysis was done separately for each of the two years of this study. While the distribution of individual variates for these variables was skewed (see above), the mean values used in this analysis were approximately normally distributed (Shapiro-Wilk statistic, $P > 0.05$), and their variances were homogenous (Bartlett-Box F and Cochran's C tests $P > 0.05$). I used SAS REG procedure for these analyses, with the forward selection option (SAS 1988).

Laboratory experiment.—I captured 29 female *A. keyserlingi* (penultimate instar) near the Crommelin Biological Research Station on 10 November 1984. These spiders were weighed to the nearest 0.1 mg on a Mettler balance and introduced into individual (30 × 30 × 7 cm) clear perspex (Plexiglass) containers. Two wood dowels were fixed vertically in each container with a piece of cotton thread strung between them about 2 cm from the top of the container. The spiders readily built orb webs parallel to the long axis of the containers, usually within hours of installation. A ball of moist cotton (re-wetted daily) was

placed in each container to maintain humidity. Each container had a 10 × 10 cm door on the center of one side for feeding. After the spider had constructed a web, this door could be opened and potential prey placed in the web. Any prey that was not consumed was removed after 24 h. The spiders were randomly divided into two groups. One group (low food) was fed 1 adult *D. tryoni* once every other day ($\bar{x}$ = 12 mg/feeding, SEM = 0.1 mg, n = 79). The second group (high food) was fed 4 adult Queensland fruit flies (*Dacus tryoni* (Froggatt)) once every other day ($\bar{x}$ = 48 mg/feeding). For comparison, the median biomass of prey captured on one sticky-board is 11.6 mg/day (no comparative data for captures in the natural webs of *A. keyserlingi* are available). After a female molted into the final instar, a freshly-captured adult male *A. keyserlingi* with fully expanded palps was introduced to the container. Any egg sacs were removed and weighed, and the number of eggs counted. Females that died during the experiment were removed and weighed as soon as they were discovered (usually within 12 h). At the end of the experiment (25 February 1985) the surviving females were removed and weighed.

Field experiment.—A food manipulation experiment was conducted to investigate the influence of supplemental prey on the behavior, survival and reproduction of adult female *A. keyserlingi*. On 10 December 1985, 80 adult female *A. keyserlingi* were located and their webs were mapped and marked in a corner with inconspicuous paper tags. The spiders were randomly divided into four groups: fed and marked (n = 30), fed and unmarked (n = 10), unfed and marked (n = 30), and unfed and unmarked (n = 10). The unmarked spiders in both treatment groups were included as a control for the marking procedure.

Spiders in the fed group were supplied with one meal worm (*Tenebrio molitor* Linnaeus) larva ($\bar{x}$ = 0.16 g, SEM = 0.01 g, n = 19) twice per day for four days. The web was watched until the spider had captured and wrapped the supplemental prey to confirm that prey did not escape. Spiders that were to be marked were captured in a plastic vial and anesthetized with CO^2 gas. They were then marked with four colored non-toxic paint dots in a unique combination. I judged that the small paint dots did not increase the conspicuousness of these brightly colored spiders. The spider was then released back onto its web. All spiders were found each day and if they had moved their new position was mapped and marked. A team of four observers was used to search for spiders. Spiders that disappeared were scored as missing. Any marked spiders that molted (but remained in the same web) were remarked. Freshly molted *A. keyserlingi* were easily recognizable. Female *A. keyserlingi* are quiescent at the time of molting and marked exuviae were found below the freshly molted individuals. Nevertheless, some individuals may have moved and molted, and these would have been scored as missing. Such movement was relatively rare in *Argiope trifasciata* Forskal and *A. aurantia* Lucas and the rate increased after molting (Enders 1975). Although web-invasion was possible (Riechert & Gillespie 1986; Hoffmaster 1986), many web movements of marked spiders were observed and no marked spiders were ever relocated in a web site that was previously occupied by another marked individual. The experiment was divided into three periods: pre-treatment period (4 d; 10–13 December), treatment period (4 d; 14–17 December), post-treatment (5 d; 18–22 December). G-tests of independence (2 × 2; Model II) were used to evaluate movement/mortality data from this experiment (Sokal & Rohlf 1981). Individuals were checked on seven subsequent dates (4 Jan to 10 March) and any egg cases that were found in marked webs were collected. These cases were maintained in the laboratory and the number of spiderlings which emerged from these cases was counted.

RESULTS

Natural reproduction.—I detected significant variation in reproductive output among individual female *Argiope* in the field. This was expressed by increasing the clutch size rather than egg size. Egg cases from 26 natural (no food supplementation) female *A. keyserlingi* had a mean mass of 0.095 g (SEM = 0.01 g), equivalent to 44% of a female's mass before laying ($\bar{x}$ = 0.21 g, SEM = 0.02 g, n = 29). These egg cases contained 4–750 ($\bar{x}$ = 298, SEM = 46, n = 26) eggs. For a second sample of 19 egg-cases, mass was strongly correlated with the number of juveniles that emerged (r_p = 0.99, $P < 0.001$). Thus the variation in egg case mass is almost completely explained by variation in numbers of eggs; variation in egg size is relatively unimportant. Females laid from 1–4 egg cases; the maximum reproductive output for any single unmanipu-

Table 2.—Web characteristics of *Argiope keyserlingi*. Mean ($\bar{x}$), standard error of the mean (SEM), 95% confidence interval about the mean (conf. int.).

Age/sex class	*n*	Top thread length (mm) and $\bar{x}$ (SEM, conf. int.)	Orb diameter (mm) and $\bar{x}$ (SEM, conf. int.)	Orb height (mm) and $\bar{x}$ (SEM, conf. int.)
Immature female	57	201 (14, 173–229)	118 (8, 101–134)	737 (40, 656–818)
Mature female	118	278 (12, 255–301)	185 (7, 172–199)	809 (34, 741–876)
Mature male	15	129 (29, 66–192)	65 (21, 20–111)	793 (101, 576–1009)
Classes combined	190	243 (8, 225–261)	155 (11, 143–167)	786 (25, 736–836)

lated female was 850 spiderlings (from 3 cases; 207, 258, 385).

Natural webs and prey.—Some web characteristics differed among the age/sex classes of *A. keyserlingi* (Table 2). Webs of mature females were significantly larger than those of immature females (top thread length ANOVA $P < 0.001$, orb diameter ANOVA $P < 0.001$). Webs of mature males were significantly smaller than either class of females (ANOVA $P < 0.001$). This is not surprising considering the fact that males of this species are tiny (mean mass = 0.005 g, SEM 0.001 g, $n = 15$) and rarely feed. The sticky orbs of all classes were at similar heights (ANOVA, *ns*).

The mean mass of 31 natural prey items was 0.04 g (SEM = 0.01 g), ranging from small gnats and mosquitos (<0.001 g) to a large predatory fly (Diptera: Asilidae, 0.12 g). The size distribution (six categories) of these prey was compared to that of potential prey captured on the sticky boards ($n = 1783$, Fig. 2). The spiders captured significantly more large prey ($\chi^2 = 365$; $df = 5$; $P < 0.001$). Large prey (>0.05 g) constituted 26% of *Argiope* prey but only 0.9% of potentially available insects. Prey were also compared to taxonomic assignment (by order, 10 categories); significantly fewer flies (all Diptera combined) and more wasps (Hymenoptera combined) were captured by the *Argiope* than the sticky boards ($\chi^2 = 254$; $df = 9$; $P < 0.001$). Flies made up 19% of *A. keyserlingi* prey but 81% of potential prey. Hymenoptera made up 29% of *Argiope* prey but only 4% of potential insect prey.

Spider density.—I calculated density for both 1984/85 and 1985/86 on each of the 16 study plots. This estimate is based on the mean number of spiders/plot for all censuses when spiders were active. The mean density in 1984/85 was 150 spiders/ha (SEM = 29, $n = 16$) and in 1985/86 it was 97 spiders/ha (SEM = 24, $n = 16$). There was considerable variation across the 16 study plots; 1984/85 coefficient of variation (CV) = 76%, 1985/86 CV 94% (Table 1). Density patterns across plots were consistent between years ($r_p = +0.81$; $P < 0.01$).

Argiope keyserlingi density was not related to any of the tree or large shrub variables, although it was significantly correlated with total numbers of small shrubs (1984 $r_p = +0.74$, $P < 0.001$; 1985 $r_p = +0.62$, $P < 0.01$). This relationship is primarily due to a strong correlation with *Xanthorrhoea resinosa* numbers (1984 $r_p = +0.88$, $P < 0.001$; 1985 $r_p = +0.86$, $P < 0.001$). *Xanthorrhoea* plants are a favored web site for *Argiope*. Principal component analysis generally

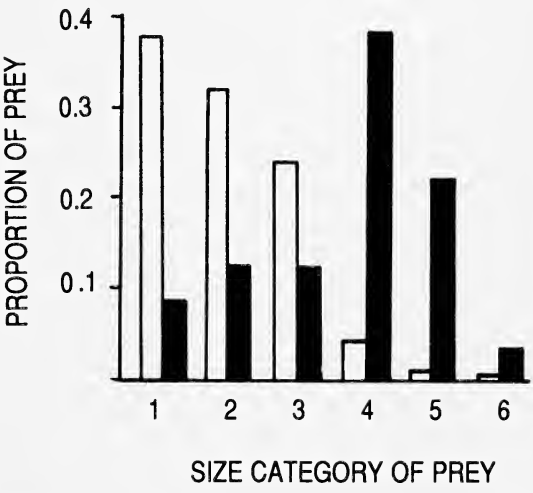

Figure 2.—Relative proportions of prey in six biomass categories. The vertical scale is the percentage of the sample which belongs in the size category. The six categories (horizontal scale) are: 1. 0–0.001 g; 2. >0.001–0.005 g; 3. >0.005–0.01 g; 4. >0.01–0.05 g; 5. >0.05–0.1 g; 6. > 0.1 g. The open bars represent the proportions of potential prey in the sticky-board samples ($n = 1783$), the solid bars represent the proportions of prey captured and consumed by *Argiope keyserlingi* observed in the field ($n = 31$).

Table 3.—Results of autocorrelation analysis for prey sampling variables. The values in the body of the table are the mean correlation for lag = 1 among all dates (1984/1985 $n = 5$, 1985/1986 $n = 4$). None of the individual correlation or mean correlation values are statistically significant. Large prey have a total body length >5 mm.

Year	Numbers	Number large prey	Biomass
1984/1985	−0.04	+0.002	+0.08
1985/1986	+0.07	+0.08	+0.04

failed to clarify the relationship between vegetation and spider density. *A. keyserlingi* density was correlated with principal component axis 3 of the vegetation analysis (1984 $r_p = +0.69$, $P < 0.01$; 1985 $r_p = +0.71$, $P < 0.01$). This axis was positively weighted on numbers of larger broadleaf trees (higher canopy) and *Macrozamia* density, both factors are indicative of a mesic microenvironment. This axis, however, explains only about 12% of the variation in the vegetation data. Neither the first nor second principal component axis was significantly correlated to spider density. Spider density was negatively correlated with plot elevation (1984 $r_p = -0.67$, $P < 0.01$; 1985 $r_p = -0.65$, $P < 0.01$). This feature covaried with vegetation characteristics, probably because the lower plots were nearer a small creek and supported lush shrub growth.

Relationship to prey.— *Temporal patterns*: Appearance of foraging spiders on the study area was slightly delayed during the spring of 1985/86, possibly due to an unusually cool fall (Fig. 1B). Despite this, the date of first appearance and general phenology of *Argiope* during the four summers from 1983/84 through 1986/87 were all quite similar despite unusual patterns of rainfall. There was a drought prior to the summer of 1983/84 and unusually heavy rains during the spring (November and December) of 1984 (Fig. 1C).

Seasonal abundance patterns of potential prey, as revealed by the sticky board samples (NUMB, NBIGS), exhibited significant variation among sampling dates (Repeated-measures ANOVA randomization test $P < 0.001$). This seasonal pattern of variation was consistent for corresponding sampling dates during the activity period of *A keyserlingi* between years (NUMB $R_s = +0.90$, NBIGS $R_s = +0.80$). Although the pattern of seasonal variation in potential prey biomass (BIOM) was also significant (Repeated-measures ANOVA randomization test $P < 0.001$), it was not consistent between years (BIOM $R_s = -0.40$, Fig. 3). The pattern of *A keyserlingi* seasonal abundance (averaged across plots) was positively correlated with all three prey variables for 1984/85 (NUMB $R_s = +0.90$, BIOM $R_s = +0.60$, NBIGS $R_s = +0.50$). This comparison for the 1985/86 season revealed a positive correlation between spider and prey numbers (NUMB $R_s = +0.90$, NBIGS $R_s = +1.0$), but not between spider numbers and prey biomass (BIOM $R_s = -0.10$). Overall, the general seasonal phenology of *A. keyserlingi* was related to the seasonal pattern of abundance of potential prey.

Relationship to prey.—*Spatial patterns*: Spatial patterns of distribution of potential prey numbers (NUMB, NBIGS) across the 16 study plots exhibited significant variation (Repeated-measures ANOVA randomization test $P < 0.05$). Spatial variation in biomass (BIOM) across plots was not significant (Repeated-measures ANOVA randomization test $P = 0.08$). The spatial patterns were not consistent between years (NUMB $R_s = +0.26$, BIOM $R_s = -0.26$, NBIGS $R_s = +0.16$; all *ns*). Autocorrelation of the three prey variables using a lag of 1 (comparing a month with the preceding month) with the 16 plots as replicates, detected no significant correlations (Table 3). Thus the spatial patterns of variation in prey across plots were not even consistent from month to month (Fig. 3). As concluded above *A. keyserlingi* density on the plots was very consistent, and it is therefore not surprising that there was no relationship between *A. keyserlingi* on the plots and any of the potential prey variables when all dates are combined. A correlation ma-

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Figure 3.—Summary of biomass of potential prey captured on sticky boards during the two sampling years (1984/1985, 1985/1986). Each dot represents the mean biomass captured on the four sticky boards on that plot for that sampling date (horizontal scale). The vertical scale is biomass in mg plotted on a log scale. The 16 graphs correspond to the 16 field sampling plots. Note that there is no consistent pattern across dates or plots, and that no plot had consistently high or low potential prey captures.

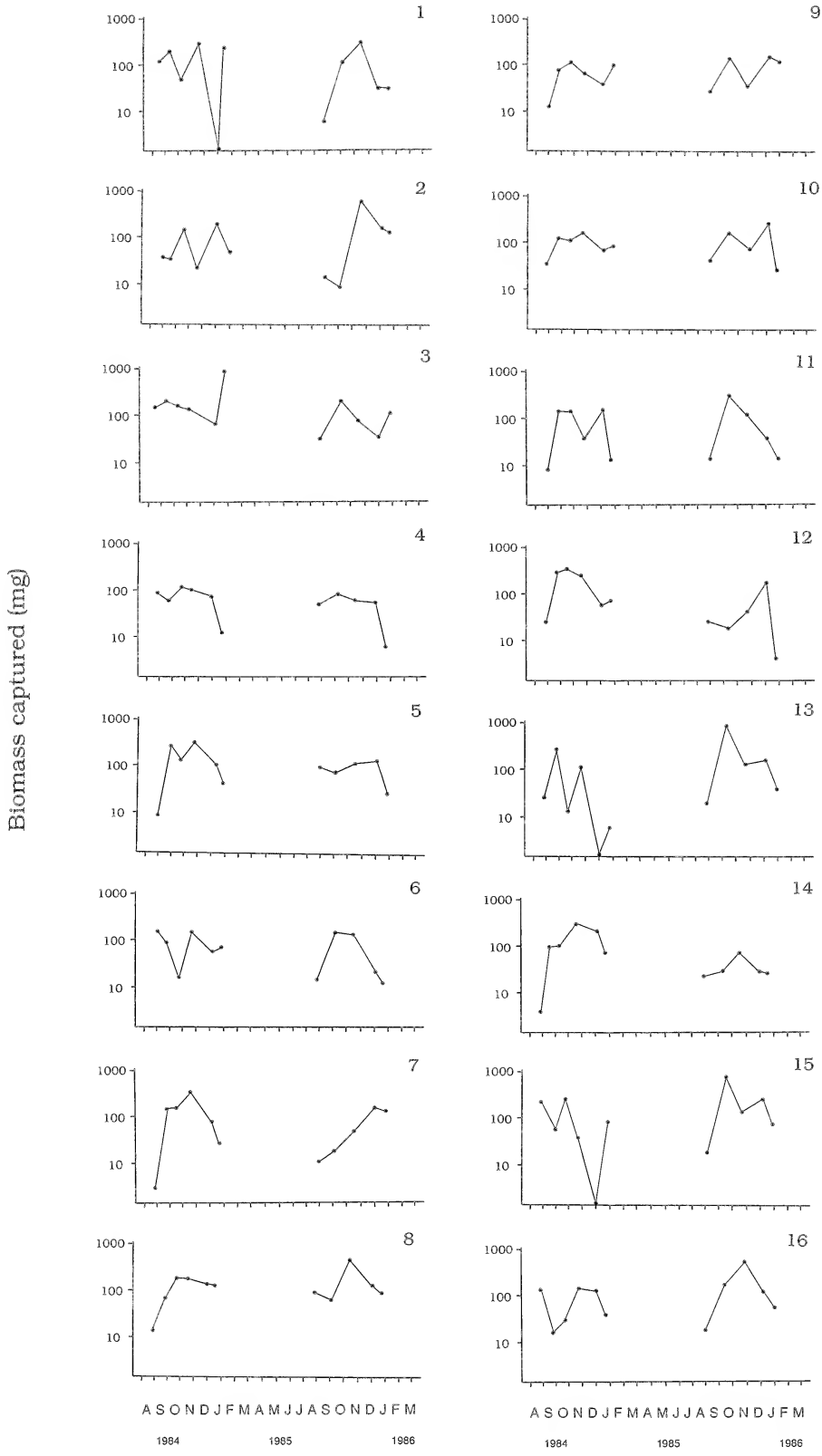
Biomass captured (mg)
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
1000
100
10
A S O N D J F M A M J J A S O N D J F M
1984
1985
1986
Sampling Date

Table 4.—Results of stepwise multiple correlation analysis of habitat and prey variables against the density of *Argiope keyserlingi* for the two study years.

Variable entering model	Partial r^2	Cumulative r^2	Significance $P <$
1984/1985 season			
Xanthorrhoea density	0.77	0.77	0.0001
Plot elevation	0.10	0.87	0.01
Prey biomass	0.05	0.92	0.05
Macrozamia density	0.02	0.94	*ns*
1985/1986 season			
Xanthorrhoea density	0.75	0.75	0.0001
Plot elevation	0.08	0.83	0.05
Total large shrub density	0.01	0.84	*ns*
Macrozamia density	0.01	0.85	*ns*

trix between spider density and potential prey variables for all date and plot samples (data not combined for rows or columns, thus all combinations calculated separately) revealed no significant correlations.

Stepwise regression analysis.—This analysis simultaneously compares the relationships between habitat and potential prey patterns and their correlation with variation in *A. keyserlingi* numbers on the study plots. The analysis revealed that habitat features were far more important predictors of spider distribution (Table 4). For both years the number of *Xanthorrhoea* entered the model first, this factor alone explained 77% and 75% of the variation in spider density for 1984/85 and 1985/86. Again for both years plot elevation was the next factor to enter explaining an additional 10% and 8% of the variation in spider numbers. All three of the potential prey measures combined explained only 6.7% of the variation in spider density in 1984/85 and <1% in 1985/86. The clear conclusion from this analysis is that habitat characteristics were a better predictor of spider density than measures of potential prey on the same plots.

Laboratory experiment.—All laboratory females mated with the males presented to them. Females maintained under the high-food treatment increased by an average of 49% of their initial mass, while those maintained under the low-food treatment did not significantly change in mass (Table 5). Of the 15 high-food treatment females, 12 produced egg cases; these females had a total reproductive output similar to that measured in the field (Table 5; *t*-test, *ns*). Only 7 of 14 females maintained under the low-food treatment produced egg cases. These females had a reproductive output significantly lower than the high-food treatment group (Table 5; *t*-test, $P < 0.05$).

Field experiment.—There were no differences in web-site movement or disappearance of marked and unmarked females, so these two categories were combined for subsequent analyses. There were no differences in the proportion of females moving between the fed and unfed groups during the pre-feeding (control) period. Significantly fewer females supplied with supplementary food moved during the feeding and post-feeding periods (G-test, $P < 0.001$; Fig. 4). Of those females that moved, there was no difference in distance moved between treatment groups (combined $\bar{x} = 1.3$ m, SEM = 0.2 m, $n = 65$).

There was no significant difference between survival (as estimated by the disappearance of individuals) of the fed and unfed groups during the pre-feeding (control) period. There was a difference in the proportion missing during the feeding period: more unfed individuals van-

Table 5.—Reproduction of *Argiope keyserlingi* in the laboratory and field. The "high food" treatment averaged 48 mg/feeding and the "low food" group averaged 12 mg/feeding. A sample of females observed in the field is included for comparison. For these females the number of juveniles was estimated (=number eggs counted).

Treatment group	*n*	$\bar{x}$ change in mass (SEM)	$\bar{x}$ number of egg cases per female	Total number of juveniles emerged per female (SEM)
High food	15	+0.103 (0.04)	1.2	293 (57)
Low food	14	−0.031 (0.01)	0.6	120 (39)
Field	26	no data	1.4	367 (46)

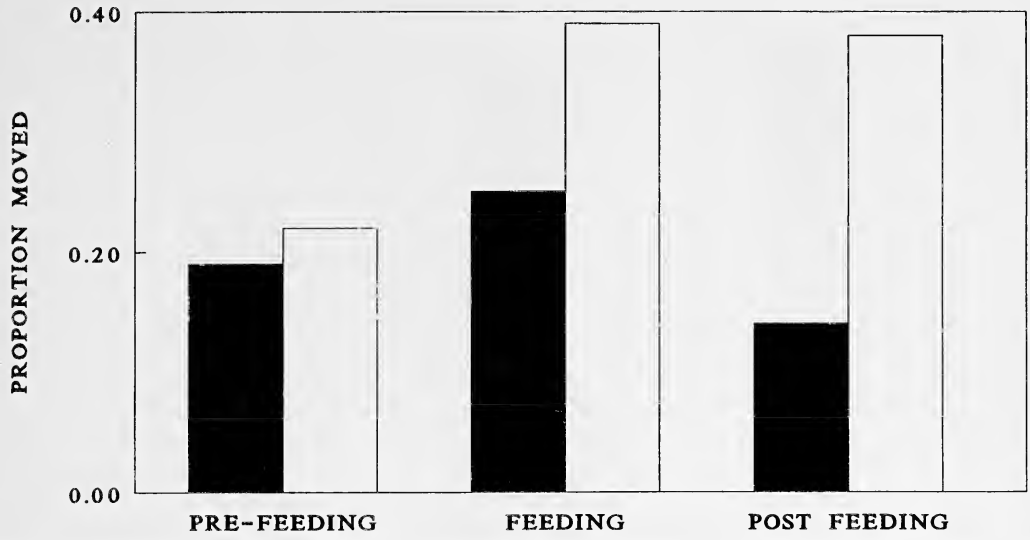

Figure 4.—Influence of the field food-supplementation experiment on *Argiope keyserlingi* movement. The data are partitioned into three periods: 1. the pre-feeding control period of four days, spiders were marked and observed but not manipulated; 2. the feeding period of four days where ½ of the individuals (all adult females) were provided with supplementary food; 3. the post-feeding period of five days where the manipulation ceased but the spiders were monitored. Data are the totals at the end of each period. The solid bars represent the spiders that were provided with supplemental food, the open bars represent control spiders. Each treatment group began with 40 spiders; sample sizes declined between periods because of spider mortality (Fig. 5).

ished, but this difference was not statistically significant (G-test, *ns*; Fig. 5). This difference was more apparent during the post-feeding period (Fig. 5) and it was statistically significant (G-test, $P < 0.001$).

Of the spiders surviving at the end of the season, 41% of the fed group produced at least one egg case whereas only 25% of the unfed group did so (Table 6). There was no significant difference between treatment groups in either the number of spiderlings per egg case or the total number of spiderlings per female (Table 6). Several of the females from each treatment group captured large prey items (in addition to the supplemental food). One of the no-supplementation females captured an unusually large prey item (large Asilid fly). This fly represents the largest single prey item recorded during this study (0.12 g), and this spider also had the highest reproductive output recorded from a female *A. keyserlingi* during this study (850 spiderlings from three egg cases). If this exceptional female is removed from the analysis, the reproductive output per female among the experimental females that were provided with supplementary food is greater than the reproductive output of those which were not fed (Table 6).

DISCUSSION

Three lines of evidence indicate that relative foraging success largely determines differences in survival and reproduction patterns among female *A. keyserlingi*. First, individual females kept in the laboratory showed a direct response to feeding treatment. The high food treatment females grew larger and were more fecund than those females maintained on the low food diet. Second, twice as many females provided with supplementary food in the field experiment succeeded in completing at least one egg case. In addition, if the single unfed female which happened to capture a very large prey item is discounted, there would have also been a significantly greater reproduction among fed females. In one sense, the exception proves the rule; this individual captured the largest prey item observed in the study and exhibited the record highest reproductive output. Foraging success is unpredictable but crucial to female *A. keyserlingi*. Another conclusion from the field experiment is that mere survival is not sufficient to insure successful production of eggs or juveniles. Only 25% of the surviving females that were exposed to natural prey abundance actually produced egg

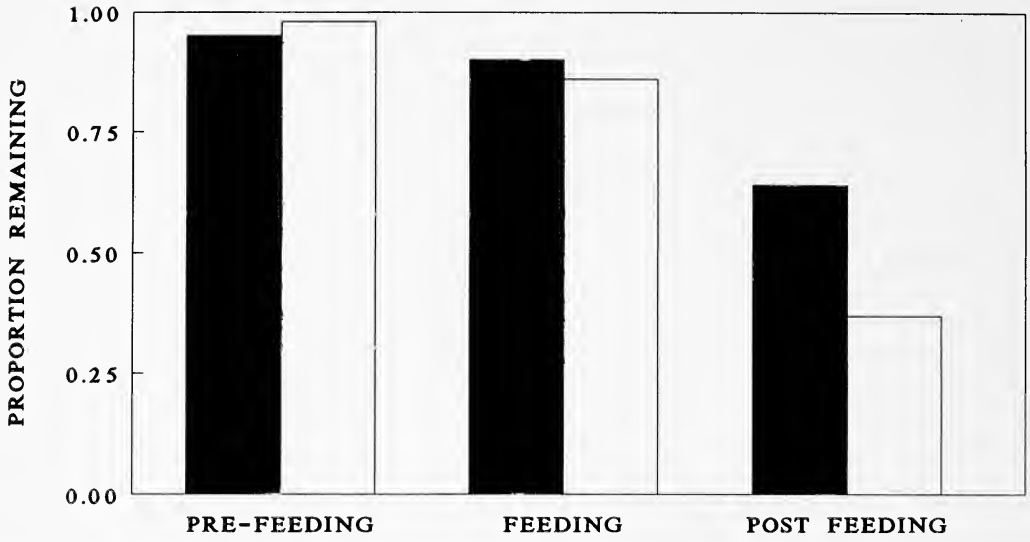

Figure 5.—Influence of the field food-supplementation experiment on *Argiope keyserlingi* survival. The data are partitioned into three periods: 1. the pre-feeding control period of four days, spiders were marked and observed but not manipulated; 2. the feeding period of 4 days where ½ of the individuals (all adult females) were provided with supplementary food; 3. the post-feeding period of five days where the manipulation ceased but the spiders were monitored. Data are the totals at the end of each period. The solid bars represent the spiders that were provided with supplemental food, the open bars represent control spiders. Each treatment group began with 40 spiders. Because of the intensive search effort by five observers and the relatively small area of suitable habitat, disappearance is probably a good measure of survivorship. Individuals classified as "absent" were assumed to be dead.

cases. Third, the mortality rate among *Argiope keyserlingi* was lower for individuals provided with supplementary prey in the field. Mortality was assessed by disappearance; it is possible that if some spiders moved and were not re-located they would have been misclassified as dead. Because there were four observers searching a limited patch of relatively sparse habitat, I believe that few individuals of this conspicuous spider were missed.

What could cause increased mortality? It is possible that individuals with poor foraging success starved to death, but this seems unlikely. Individuals maintained in the laboratory survived on low food for a period well beyond the scope of this experiment. When individual *Argiope* die from starvation, they are found hanging from their webs or in the vegetation below. Dead spiders were rarely found. It seems much more likely that they suffered increased risk of predation. Visually hunting predators, including diurnal birds and wasps (*e.g., Cryptocheilus* sp.), are more likely to notice moving spiders. Vollrath (1985) suggested that movement to a new

Table 6.—Fecundity of *Argiope keyserlingi* females from field manipulation experiment. Figures based on the number of females that remained and produced at least one egg case (number that laid any eggs). The number of juveniles was based on a total count of active juveniles that emerged (all cases combined). Unfed (subset) treatment group recalculated excluding the single female that captured the record largest natural prey item.

Treatment group	Original *n*	Number at end of experiment	Number that laid any eggs	Number of egg cases per fecund female ($\bar{x}$)	Number of spiderlings per case $\bar{x}$ (SEM)	Number of juveniles per female $\bar{x}$ (SEM)
Food added	40	22	9	1.2	293 (34)	147 (66)
Unfed	40	16	4	2.0	290 (43)	145 (137)
Unfed (subset)	39	15	3	0.6	294 (122)	98 (118)

web site increased the risk of predation for *Nephila clavipes* (Linnaeus), and that individuals provided with supplementary prey moved less and suffered a lower rate of mortality. As adult female *Argiope keyserlingi* become sated with food their behavior changed; they ceased rebuilding the sticky-orb each morning and they moved to a retreat in a curled leaf near the upper attachment point of the web. This shift probably made them far less obvious to a predator hunting for spiders in a web. Several of the adult females that were in the food supplementation treatment group quit foraging after only two days of extra food. These spiders remained in their retreat until they laid eggs. Increased foraging success would thus reduce the apparent exposure of a female to predators which search webs, and might account for the lower mortality in the fed group that was evident only towards the end of the experiment because the mortality effect would be cumulative (Fig. 5).

Do patterns of activity and habitat selection in *A. keyserlingi* reflect prey abundance or habitat, or both? There is some evidence from this study that the annual phenology of *Argiope keyserlingi* is related to seasonal variation in prey abundance. Spatial distribution of spider density was, however, not related to prey abundance patterns. If the data are analyzed treating each date and plot as a separate sample, there seems to be little relationship between *A. keyserlingi* and potential prey. *Argiope* are most active when prey are most abundant, but not necessarily in sites with highest prey numbers. There was no serial-autocorrelation in the sticky-board insect samples in this study, suggesting that prey were unpredictable in time and space. The inconsistency in prey numbers between years across plots apparently obscures any more general seasonal relationship between spider density and prey abundance. In a comparison of *Argiope aurantia* Lucas and *A. trifasciata* (Forskal), McReynolds & Polis (1987) concluded that differences in habitat and prey handling abilities explained the small dietary differences between these two species. Differences in diet reflected both seasonal change in the prey available as well as the size relationships between growing spiders and the prey that they were capable of handling (McReynolds & Polis 1987). Few of the measured web characteristics were correlated with the taxa of prey which were captured (McReynolds & Polis 1987). My results with *A. keyserlingi* appear consistent with those of McReynolds and Polis insofar as the fact that prey captured seem to reflect seasonal prey availability. I do not have any comparable information on individual prey capture rates, or the relationship between spider size and prey captured.

Although *A. keyserlingi* reproduction seems to be closely tied to the biomass of prey captured, there was no evidence indicating that *A. keyserlingi* exerted control over prey density. This situation resembles a donor-controlled system (Pimm 1982). Pimm (1982) suggested that this sort of relationship should be rare (with the exception of detritivores). The fact that *A. keyserlingi* abundance appeared to have had little effect on prey density might be because this orb-weaving spider was only one of many predators that influenced insect abundance in the study area. Alternatively, this may be related to the fact that the density of *Argiope keyserlingi* was low compared to estimates for other *Argiope* species which average 40 to 50 times higher than those measured in this study (Olive 1980; Brown 1981; Horton & Wise 1983). Thus there may be too few *Argiope keyserlingi* present to have exerted control over insect abundance.

Argiope keyserlingi density was related to general habitat features, especially those associated with web-site availability (*e.g., Xanthorrhoea* density). The importance of *Xanthorrhoea* shrubs as web sites may be related to the fact their structure, with a brush of long (1 m) narrow (1–6 mm) leaf blades spreading radially from a central trunk, provides an infinite gradation of gap sizes which can accommodate webs of many sizes and orientations. There was no correlation between these preferred sites and potential insect prey abundance. If prey are not predictable and there is high mortality among adult females in their webs, it is possible that *Argiope* choose web-sites as much to avoid predation as to maximize prey capture rate. In light of this, it would be interesting to investigate the influence of web position on the risk of predation.

Overall, these data support the idea that vegetation structure is the chief determinant of web-site choice for orb-weavers, rather than prey availability (Enders 1973; Colebourn 1974). Three of four orb-weaver species studied by Pasquet (1984) exhibited a clear relationship between density and habitat structure, while only two species built webs where prey abundance was highest. Furthermore, vegetation structure but not prey availability was found to be a very important predictor of spider community structure (Greenstone 1984). In a study comparing the

spider assemblages on three continents, Rypstra (1986) found that vegetation structure was the best predictor of spider activity. Prey abundance was also significantly correlated with spider activity at each locality (Rypstra 1986). Riechert & Gillespie (1986) reviewed the basis for web-site selection taken from the literature including data from 14 species of araneids. Vegetation was a web-site selection criterion for 12 of these 14, while prey abundance was important for only 5 of the 14 species. In the sheet-web building agelenid *Agelenopsis aperta* (Gertsch), web sites are the subject of intense intraspecific competition; and there was a clear positive correlation of favorable web sites with both physical and prey-capture criteria (Riechert 1974, 1976, 1977, 1979, 1981). It is clear that in cases where vegetation and potential prey covary, inference about their relative importance is difficult. Rypstra (1983) demonstrated that both web-substrate complexity and prey abundance are important to equilibrium spider density within enclosures. In this case, prey appear to be a more important determinant, but this result is partially explicable by reduced interspecific predation and cannibalism among the spiders in the enclosures maintained under the high food regimes.

My results reinforce the general conclusion that vegetation structure is an important predictor of orb-weaving spider abundance. Prey abundance appears to be of lesser significance in relation to spider density, but this may not indicate that it is less important to the spiders. As Rypstra (1986) points out, vegetation is easier to quantify; and I would add that it is probably less variable in space and time than insect abundance. Perhaps the difficulties involved in precise quantification of prey availability are an important confounding factor in broad-scale community analyses. Prey variability is real and it is possible that spiders are constrained to use a more reliable factor (vegetation) in their efforts to select profitable foraging sites. An indication that prey encounters influence *A. keyserlingi* behavior is that web-site movement was related to success in capturing prey. Individuals provided with supplementary prey were more sedentary (Fig. 4). Similar results have been observed in other orb-weaving spiders in the field (Olive 1982; Janetos 1982; Vollrath 1985). In contrast, there was no relationship between dietary experience and movement in laboratory experiments on *Nephila clavipes* (Vollrath & Houston 1986).

Gillespie & Caraco (1987) found that individuals of *Tetragnatha elongata* Walckenaer in a prey-rich environment actually moved more than those inhabiting a relatively depauperate area. Their results appear consistent with the predictions of a risk-sensitive foraging model where movement will increase as prey availability exceeds an appropriate physiological requirement. The behavior of *Tetragnatha elongata* apparently does not match a second model described in their paper, which predicts that spider mobility would be inversely related to prey availability. The key difference between these two models was whether a foraging spider used capture success information to predict the best strategy. According to these authors the first model assumes that temporal variation in prey abundance makes it difficult for a forager to predict spatial prey distribution. Hence if prey availability is high, spiders will benefit by sampling several localities. Results for *A. keyserlingi* appear to conflict with Gillespie and Caraco's result. Temporal variation in prey abundance appeared to mask spatial predictability, and prey abundance was limiting to female *Argiope*. Nevertheless, individual female *A. keyserlingi* moved more often when their foraging success was poor.

Interpretation of the present study depends upon the scale of observation. On a broad scale, there was a positive relationship between *Argiope keyserlingi* seasonal phenology to temporal prey-abundance patterns. On a finer scale, there was little relationship between prey abundance and the number of active foraging spiders on individual sampling plots. At this scale, spider density seems to be related to the availability of preferred sites for the construction of webs. At the scale of individuals, the history of foraging success predicted both survival and reproduction, and had a dramatic influence on behavior.

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CONSTRAINTS AND PLASTICITY IN THE DEVELOPMENT OF JUVENILE *NEPHILA CLAVIPES* IN MEXICO

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ABSTRACT: The large, orb-weaving spider *Nephila clavipes* is found in a diversity of habitats within a narrow latitudinal range in Mexico. This allowed nearly simultaneous study of post-embryonic development of six disjunct populations in dissimilar environments. A common-garden laboratory study utilizing juveniles collected in four sites reinforced the conclusions from the field. The developmental parameters influencing growth in size at ecdysis did not vary within or among populations and may be genetically determined. Although very small juveniles exhibit variation in the growth per ecdysis, larger juveniles exhibit very little variation. These data, compared to data from field and laboratory studies of other tropical populations of *N. clavipes,* indicate that growth per ecdysis is highly constrained. Thus, this developmental parameter establishes a developmental trajectory that may be genetically determined and therefore subject to natural selection.

RESUMEN: La araña *Nephila clavipes,* tejedora de telas orbiculares, se encuentra en habitats diversos en México dentro de un límite angusto de latitúd. Eso permitió estudios casi simultaneos de ontogenia de juveniles en seis poblaciones desunidos en ambientes distintos. Un estudio del laboratorio utilizando juveniles colectados en cuatro sitios fortalece las conclusiones del campo. Los parámetros ontogenéticos determinando el crecimiento por muda no varió dentro ni entre poblaciones, y posiblemente son geneticamente determinados. Aunque juveniles muy pequeños mostraron variación en el crecimiento por muda, juveniles mas grandes no mostraron variación en este parámetro. Estos datos, combinados con datos de estudios de otras poblaciones en el laboratorio y en el campo, indican que el crecimiento por muda esta muy constreñido. Asi, este parámetro establece una trayectoria ontogenética que posiblemente sea geneticamente determinado y sujeto a selección natural.

Determining how environmental factors influence life history requires determination of the developmental parameters at each life-history stage and examination of whether the parameters are phenotypically plastic, responding to the environment, or are genetically determined (Caswell 1983, Via & Lande 1985, Pease & Bull 1988). The development of the large orb-weaving spider *Nephila clavipes* (Linnaeus) (Araneae: Tetragnathidae) can be expressed as a group of interdependent parameters with varying degrees of phenotypic plasticity (Higgins 1992a). Experimental trials showed that weight gain and intermolt interval duration responded to shifts in food availability, but growth per ecdysis did not (Higgins pers. obs.). The duration of the intermolt interval was found to be correlated with the size of the spider and apparently reflected the length of time the individual required to achieve the minimum weight necessary to molt to the next instar. In field studies, whereas the rate of weight gain and the number of juvenile molts varied with habitat within and among populations, the growth per ecdysis did not vary within a population or between two populations in the tropics (Higgins 1992a). The constraints imposed upon development by the constant growth per ecdysis were countered by phenotypic plasticity in other developmental parameters, particularly the number of instars, generating variation in size and age at maturity (Higgins 1992a; Higgins pers. obs.).

The previous studies utilized a range of sites with widely differing physical and biological conditions including photoperiod, making it difficult to distinguish the relative influence of different ecological factors on post-embryonic development. In order to better understand the environmental influence on development, a second field study was undertaken, utilizing the diversity of habitats in which *N. clavipes* is found in Mexico. Choosing sites within a 1° latitude range eliminated variation in photoperiod among sites and allowed nearly simultaneous study of populations experiencing very different environments.

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In order to more fully explore the plasticity and constraints of development, juveniles from the four most distinct habitats were brought into the laboratory in a common-garden experiment.

Common-garden experiments, where individuals from different environments are held in a common environment, allow preliminary differentiation between those parameters that are apparently genetically determined and those that are phenotypically plastic (Wise 1987). Parameters that are genetically determined and vary among populations will express similar variation in the laboratory among individuals from those populations. In contrast, parameters that are phenotypically plastic and vary among populations will not vary in the laboratory among individuals from different populations. The combination of laboratory and field observations thus allows distinction between constrained, potentially genetically determined, parameters and phenotypically plastic parameters.

METHODS

Populations studied.—Spiders were observed in six sites spanning Mexico from the Veracruz coast to the Jalisco coast. Three sites were in Veracruz: Playa Escondida, Nanciyaga, and Fortín de las Flores. One site was in the high altitude desert valley of Tehuacán, Puebla. Two sites were west of the central plateau: Arroyo Frio, Michoacan, and Chamela, Jalisco. In 1989 I traveled to Playa Escondida, Nanciyaga, Fortín de las Flores, Arroyo Frio, and Chamela. In 1990, I studied spiders in Playa Escondida, Nanciyaga, Fortín de las Flores, Tehuacán, and Chamela. Because these sites varied only 1° latitude, there was no significant difference in photoperiod among them. However, the sites varied in many environmental parameters including type and degree of seasonality, and prey capture rates (Table 1).

Playa Escondida and Nanciyaga are privately owned forest preserves about 13.5 km apart on the Veracruz coast, separated by cattle ranches. Both have wet climates with relatively cool winters. Playa Escondida is approximately 1 km from a previous study site, the biological station "Los Tuxtlas" (Higgins 1992a, b). The *N. clavipes* population at the latter site disappeared shortly after dispersal of juveniles early in 1989, and the study was continued at Playa Escondida. The third Veracruz site, Fortín de las Flores, is a mid-altitude area of coffee plantations (Benton & Uetz 1986). This site is cooler and experiences stronger winters with minimum temperatures as low as 0 °C. On the western, dry side of the Sierra Madre Oriental in the valley of Tehuacán, I studied the spiders at the Secretaria de Ecología y Desarrollo Urbano cactus garden near Zapotitlán Salinas, Puebla. Annual rainfall in Tehuacán is very low and there is a relatively cold winter. Climatological data are not available for Arroyo Frio, located near Perdenales in southwestern Michoacan. The area is seasonally dry and, due to the altitude, seasonally cool. However, there is a permanent stream through the site that maintains high relative humidity within the arroyo where the spiders are found. On the Pacific coast of Jalisco, the spiders were studied at Chamela field station, owned and run by the Instituto de Biología, Universidad Nacional Autonoma de Mexico (UNAM). This site is seasonally dry but never cool. Spiders were found during the rainy season at all sites, but are facultatively bivoltine at both coastal Veracruz sites (Higgins in press). There was no second generation at these sites in 1989 and 1990, so data are presented from only the rainy season.

Rates of prey capture were estimated through trap-line surveys (Turnbull 1960). The spiders in Playa Escondida captured fewer prey than the spiders at other sites (Table 1) (Higgins pers. obs.). Predation load, estimated as the proportion of juveniles less than 0.5 cm leg I tibia + patella length that abandoned intact orb webs following predator attack (as in Higgins 1992b), was higher in Tehuacán, Arroyo Frio, and Chamela, but the differences were not significant (Higgins pers. obs.).

I traveled alternately east and west from Mexico City, visiting inland sites both on my way to and returning from the coastal sites. The visits at the coastal sites were slightly longer than visits to the inland sites. The combination of longer visits at the end points and repeated visits at intermediate sites enhanced the probability of observing molts by marked individuals.

Field observations.—Field observations of individuals utilized the methodology previously described in detail (Higgins 1992a). At each site, censuses of spider abundance and size were made and web sites were flagged. Measurements, made with Helios needle-tipped calipers, included spider leg I tibia + patella length (TPL, cm), abdomen length, and abdomen width. Individuals larger than 0.5 cm TPL were marked with enamel paint on their legs. From abdomen length and width, the abdominal volume was estimated as

Table 1.—Location, climate and relative prey capture rates at each site. Annual rainfall and mean temperature were taken from the nearest weather station reported by Garcia (1973) for all sites except Chamela. Data from Chamela come from Bullock (1986 and pers. commun.). Temperatures are for the growing season. No weather data are available for Arroyo Frio. (§ Mean prey capture per 12 diurnal hours per spider (Higgins, pers. obs.), determined as in Higgins & Buskirk 1992.)

Site	Coordinates	Altitude (m)	Annual rainfall (m)	Mean temp. °C	Prey capture§
Playa Escondida	18°35′N, 95°W	0	4.5	26	low
Nanciyaga	18°35′N, 95°W	100	4.5	26	high
Fortín de las Flores	18°50′N, 97°W	1000	2.5	22	high
Tehuacán	18°20′N, 97°30′W	1200	0.3	20	high
Arroyo Frio	19°10′N, 101°30′W	1200	—	—	—
Chamela	19°30′N, 105°W	50	0.7	—	high

a cylinder. For a given TPL, abdomen volume is highly correlated with spider weight (Higgins 1992a). Each individual found on a non-viscid silk platform was assumed to be pre- or post-ecdysis (Higgins 1990). The size of the abdomen relative to the legs distinguished between these conditions: pre-ecdysis individuals have large, distended abdomens whereas post-ecdysis individuals have much smaller abdomens relative to leg length and carapace width. Collection of exuviae provided additional data for the analysis of growth per ecdysis. Post-ecdysis spiders often hang the exuvium in the barrier webs near the hub connection, and TPL of an exuvium is not significantly different from the spider size in the previous instar (Higgins 1992a). When several exuviae were present, I only measured the largest, from the most recent molt.

These data are used to compare the relationships among abdomen volume, premolt TPL, and postmolt TPL within and among the populations over the entire life-cycle of the spiders. These parameters all describe the growth per molt, and as such are not strictly independent. However, because there was a chance that spiders gain weight beyond that required to successfully complete ecdysis (particularly relevant for penultimate-instar individuals), premolt abdomen volume was compared as well as premolt and postmolt TPL. To describe growth patterns of the species in North America, data from previous studies in Texas, USA, "Los Tuxtlas", Veracruz Mexico, and Panama (Higgins 1992a) were compared to those presented here.

Common garden experiment.—In 1990, juvenile spiders from two wet and two dry sites were brought into the laboratory. The populations selected for laboratory study were Nanciyaga, Fortín de las Flores, Tehuacán and Chamela. The spiders were maintained on three dimensional frames made of two intersecting 30 cm circles made of fiberglass strips, and were free to move about the laboratory. From each site, spiders of 0.2–0.4 cm TPL were collected. Twenty-three spiders were used in the experiment, as follows: Nanciyaga (3 females, 1 male), Fortín (3 females, 3 males), Tehuacán (2 females, 4 males), Chamela (2 females, 5 males). The ratio of juvenile males to females depended upon the exact dates of collection. Later in the season, small spiders are more likely to be males (pers. obs.). In addition, three spiders escaped prior to being marked during a trip to Fortín and Tehuacán. These animals were included in the description of weight gain during the intermolt interval.

The spiders were maintained 3–4 days with only water to increase the probability of spinning when released, and were offered food immediately after a web was spun. Any spider that did not spin an orb within three days of release in the laboratory was not included in the experiment. Throughout the experiment, each spider was offered three *Drosophila virens* each day. For a period of one week, only *D. melanogaster* was available; two of these were substituted for each of the larger *D. virens* (for a total of six flies). At the initiation of the experiment, the spiders were measured (TPL, abdomen length, abdomen width), and these measures were repeated with each molting. Abdomen volume was measured every other day during the intermolt interval to monitor weight gain. The majority of the spiders were held for two molts; one individual from Fortín failed to molt a second time in the lab-

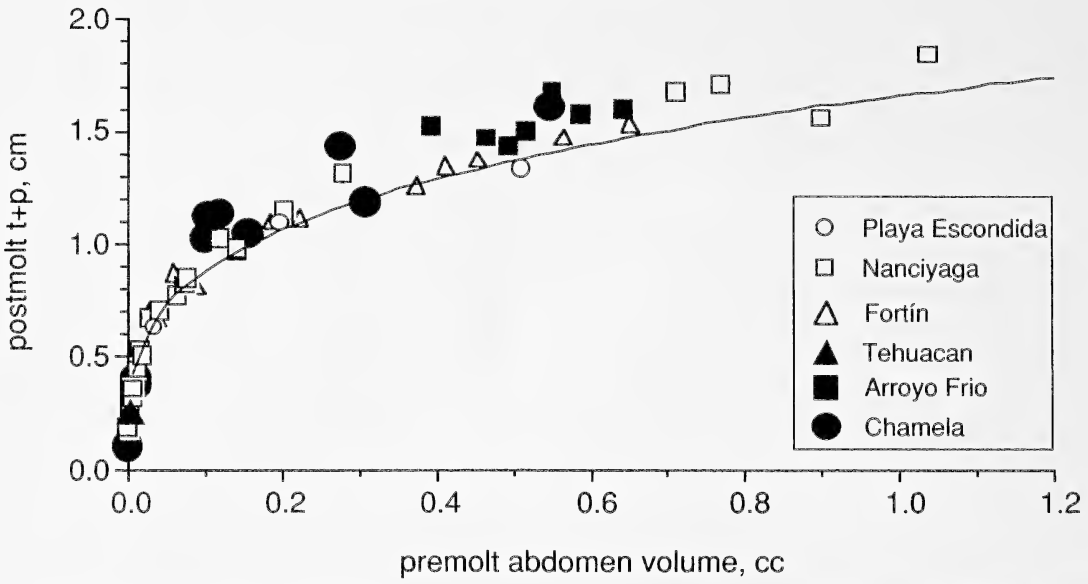

Figure 1.—Postmolt size (leg I tibia + patella length, TPL) as a function of premolt abdomen volume at all sites. Only data from juveniles and females molting to maturity are included in the graph. The curve represents a fit to the entire data set, $y = 1.66 \times {}^{0.28}$ ($R^2 = 0.99$).

oratory. Observations also distinguished those days when the spiders were foraging and had partially or wholly renewed orbs from the days immediately pre- or post-molt, when the spiders were not actively foraging. Data presented here concern the growth per ecdysis, length of the intermolt, days spent foraging during the intermolt and pattern of abdomen volume gain during the intermolt period.

Statistical analyses.—The developmental parameters examined in this study are dependent upon the size, TPL, of the individual. Therefore, all analyses tested for a significant regression between TPL and the measurement in question. If the regression analysis was significant for each population, further analysis tested for significant variation in the slope of the regression lines among populations. If there was a significant interaction of population and TPL, indicating difference in slope, then the analysis was halted (Sokal & Rohlf 1981). If the interaction terms were not significant, a final analysis of covariance (ANCOVA) with TPL as covariate tested for variation in the altitude of the line (y intercept). Lastly, if no difference was found due to population or treatment in a biologically important variable, *a posteriori* power tests were calculated to determine the minimum percent difference in the slope or intercept that could have been detected with these data.

RESULTS

Field observations.—*Abdomen volume and molting:* The relationships among premolt abdomen volume, premolt TPL and postmolt TPL vary little within or among the six populations studied. Postmolt TPL is related to the abdomen volume by a concave function, approximately a function of the cube root of abdomen volume (Fig. 1). The data are insufficient to allow comparison among the sites because recording premolt abdomen volume and postmolt TPL for the same individual was unlikely in the field.

The premolt abdomen volume is a function of premolt TPL, and males and females molting to sexual maturity do so at a lower abdomen volume compared to juveniles molting to juvenile instars. The data from Fortín included the greatest number of observations of molts to sexual maturity (Fig. 2). Penultimate instar males and females were identified as follows: almost all females of TPL greater than 1.0 cm are molting to sexual maturity (pers. obs.) and penultimate males have swollen palpi. After correcting for heteroscedasticity by taking the square-root of the dependent variable (cube root of abdomen volume), ANCOVA of the data from Fortín revealed that the differences among juveniles, penultimate instar males, and penultimate instar females were significant (TPL: $F_{(1,52)} = 1475.6$, $P < 0.001$; sex/

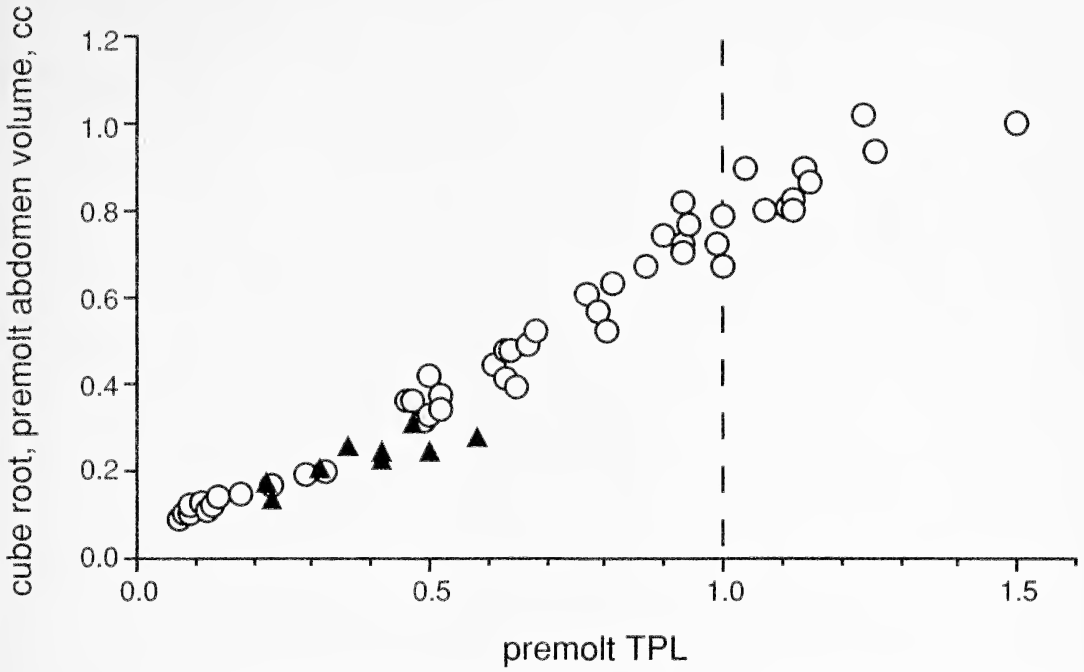

Figure 2.—The cube root of premolt abdomen volume as a function of premolt TPL (leg I tibia + patella length) for spiders in Fortín. These data include males molting to sexual maturity (= ▲) and juveniles and females (= ○). The points above premolt TPL = 1.0 cm are females molting to sexual maturity.

age: $F_{(2, 52)} = 8.85$, $P < 0.001$; interaction: $F_{(2, 52)} = 13.75$, $P < 0.001$). Separate comparison of males and females molting to sexual maturity indicated that the function of premolt abdomen volume on premolt TPL have the same slope ($F_{(1, 15)} = 2.28$, *ns*, power test: 4.1% detectable difference in slope).

Data from the remaining populations included few observations of spiders molting to maturity, so the comparison of the function of premolt abdomen volume on premolt TPL among sites utilized only data from juvenile molts. Arroyo Frio data were excluded from the final analysis because few spiders were observed in the size range of 0.5 cm–1.0 cm TPL. ANCOVA of premolt abdomen volume (to the 0.15 power) with TPL as covariate revealed that there was no difference in slope among all five sites ($F_{(4, 107)} = 1.75$, *ns*, power test: 1.8% detectable difference). The interaction term was dropped from the final ANCOVA, and this test showed that spiders in Chamela molted at a slightly but significantly lower premolt abdomen volume for their size [ANCOVA. TPL: $F_{(1, 111)} = 4283.4$, $P < 0.001$; site: $F_{(4, 111)} = 7.63$, $P < 0.001$; regressions: Chamela: $y = 0.30 + 0.54$ (TPL); remaining sites: $y = 0.32 + 0.55$ (TPL)].

Growth per ecdysis: Growth per ecdysis was compared within and among populations using regression analysis of postmolt TPL on premolt TPL. The slope of the regression line is an indication of the rate of size-specific growth. Molting to sexual maturity was presumed to affect the rate of growth at ecdysis because postmolt TPL is correlated with premolt abdomen volume, and whether the spiders were molting to maturity influenced the premolt abdomen volume. Therefore, the observations of molting juveniles, males molting to maturity, and molting females larger than 1.0 cm TPL were considered separately. Within sites, preliminary regression analyses showed that premolt and postmolt TPL were significantly correlated for juvenile molts at all sites (all $P < 0.003$) (Fig. 3). Individual ANCOVA were run to check for differences in growth during juvenile molts between years at the sites studied in both years: Nanciyaga, Playa Escondida, Fortín de las Flores, and Chamela. No significant differences were found (all $P \geq 0.12$); therefore, data from 1989 and 1990 were combined for the remaining tests. Due to small numbers of observations, the data from both years were pooled for the analyses of growth during molts to sexual maturity. Preliminary regression analyses of

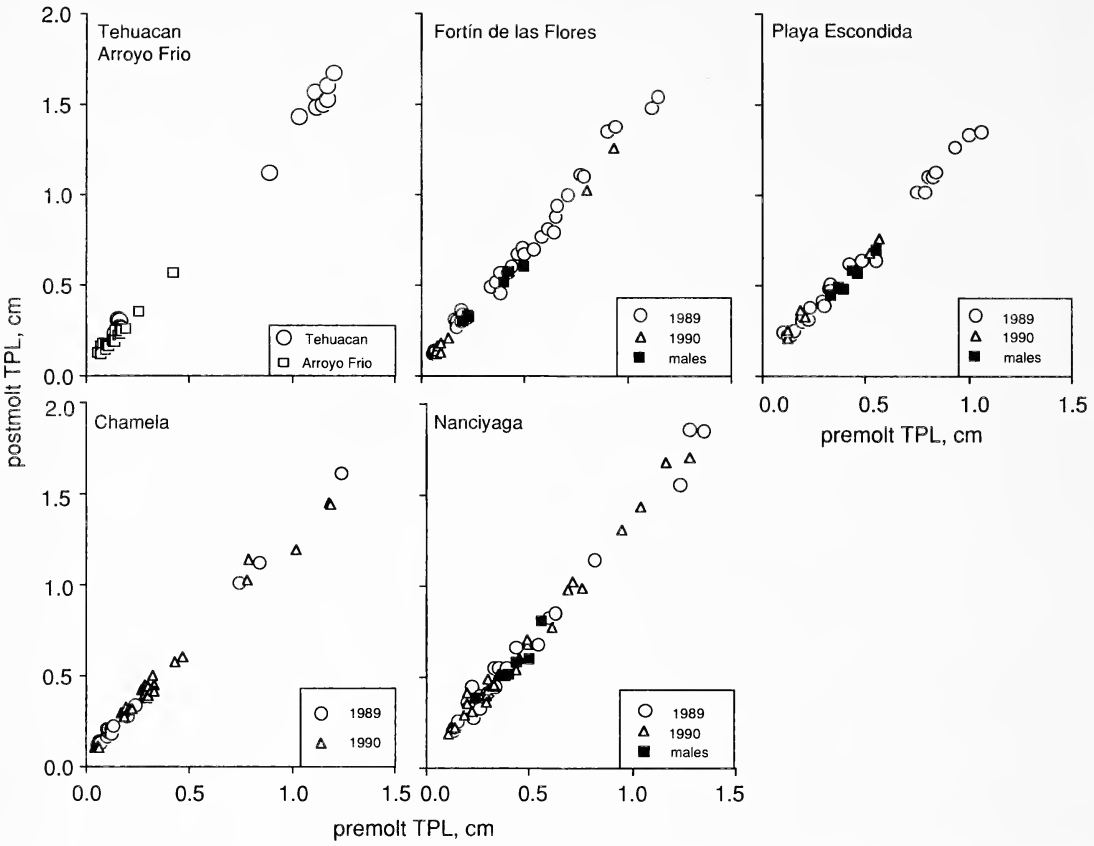

Figure 3.—Growth per ecdysis, determined as the relationship between premolt TPL (leg I tibia + patella length) and postmolt TPL for all populations observed. Arroyo Frio (1989) and Tehuacán (1990) are plotted together, all other plots contain data from two years. Males molting to maturity are indicated by solid squares (■).

postmolt TPL on premolt TPL were significant for males from Playa Escondida, Nanciyaga, and Fortín, and for females from Nanciyaga ($P < 0.02$).

Travel precluded collecting complete data sets for all populations, therefore comparison between age and size classes (juvenile, male or female) were restricted to a few sites. Data from Nanciyaga indicated that there was no difference in growth per ecdysis between juveniles and females molting to maturity (no interaction effect $F_{(1,57)} = 0.01$, *ns*; ANCOVA. TPL: $F_{(1,58)} = 1567.1$, $P < 0.001$; maturity: $F_{(1,58)} = 2.01$, *ns*). In all three Veracruz sites, males were observed molting to maturity. ANCOVA showed significantly lower growth per ecdysis (slope of the line) in males molting to maturity than in molting juveniles less than 1.0 cm premolt TPL (Table 2).

Table 2.—ANCOVA of growth per molt of juveniles and males molting to maturity in Playa Escondida, Nanciyaga, and Fortín de las Flores. (* $P \leq 0.01$, ** $P \leq 0.001$)

Factor	*df*	*F* ratio
Premolt TPL	1	419.3**
Site	2	1.26
Maturity	1	3.28
Site × premolt TPL	2	2.98
Maturity × premolt TPL	1	7.81*
Site × maturity	2	0.26
Error	133	

Comparisons made among sites for juvenile molts revealed no difference among sites in growth per ecdysis either in slope or in intercept (slope: $F_{(5,208)} = 1.98$, *ns*, power test 0.9% detectable difference; intercept: $F_{(5,213)} = 1.48$, *ns*, power test 1.9% detectable difference) (Table 3). However, these regression analyses obscure a slight non-linearity of the data. Closer exami-

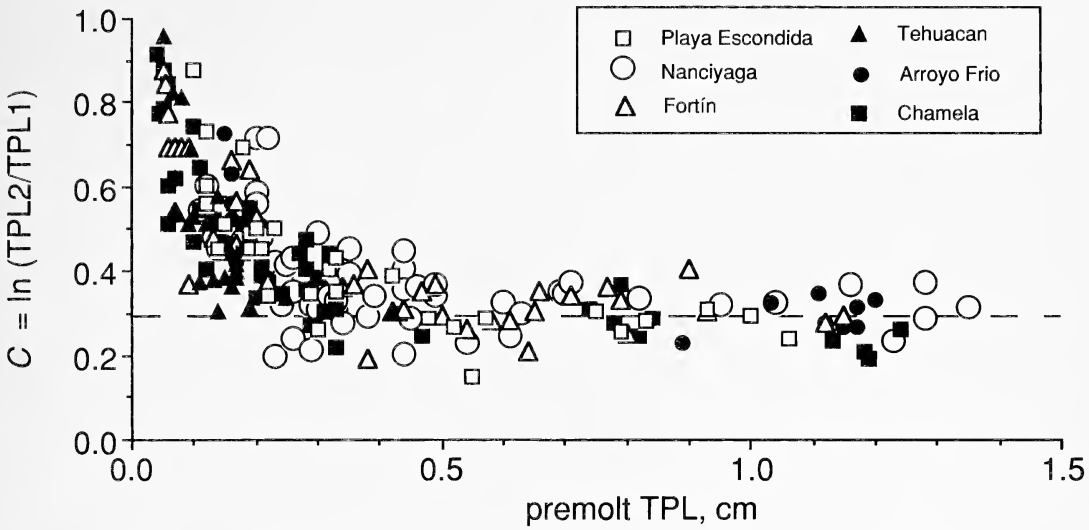

Figure 4.—The growth statistic C as a function of premolt TPL (leg I tibia + patella length). The value of C equal to the average slope of the equations of growth per ecdysis (Table 3) is indicated by the dotted line.

nation of variation in the growth per ecdysis was permitted by calculation of a growth statistic, C = ln(TPL2/TPL1). This growth statistic is related to Huxley's growth equation (1972 p. 6) as C = ln(αG) when dt = 1 instar, but it is not the same as k. Mean C is a function of the regression equation slope (ln(slope) = mean C). This transformation revealed that although C was independent of premolt TPL for larger spiders, for individuals of the first and second instars (TPL < 0.3) C was strongly dependent upon premolt TPL (Fig. 4). The data from all populations appear to fall on the same curve. The high values of C for small spiders reflect the large changes in TPL at ecdysis. Spiderlings with premolt TPL of 0.05 cm often molt to TPL of 0.11 cm, an increase of 100% or C = 0.8.m.

The data concerning juvenile growth per ecdysis can be compared to data collected in earlier studies of populations at Barro Colorado Island, Panama, at Los Tuxtlas, Veracruz, Mexico, and in southeastern Texas, USA (Higgins 1992a). The older data set did not distinguish males molting to sexual maturity. Therefore, the ANCOVA was run with juveniles of less than 1.0 cm premolt TPL and males. There was no difference among any of the tropical populations (no interaction effect: $F_{(7, 365)} = 1.67$, *ns*, power test: 2.2% detectable difference; ANCOVA. TPL: $F_{(1, 372)} = 19{,}370.4$, $P < 0.001$; site: $F_{(7,372)} = 0.99$, *ns*, power test: 4.7% detectable difference). Inclusion of observations from the University of Houston Coastal Center in Galveston County, Texas, resulted in a significant site effect on slope, reflecting the significantly lower slope of the growth per ecdysis for the Texas population (ANCOVA. TPL: $F_{(1, 425)} = 5776.6$, $P < 0.001$; site: $F_{(8, 425)} = 1.14$, *ns*; site × TPL: $F_{(8, 425)} = 4.91$, $P < 0.001$).

Table 3.—Regression equations for juvenile growth per ecdysis, where initial TPL is less than 1.0 cm. (**P < 0.001)

Site	n	Regression intercept	Regression slope	R^2	F (regression)
Playa Escondida	31	0.068	1.24	0.99	2671.1**
Nanciyaga	55	0.051	1.29	0.97	1959.7**
Fortín de las Flores	41	0.043	1.32	0.99	3150.0**
Tehuacán	24	0.053	1.19	0.96	591.0**
Arroyo Frio	17	0.078	1.25	0.99	1423.0**
Chamela	52	0.047	1.29	0.99	4743.5**

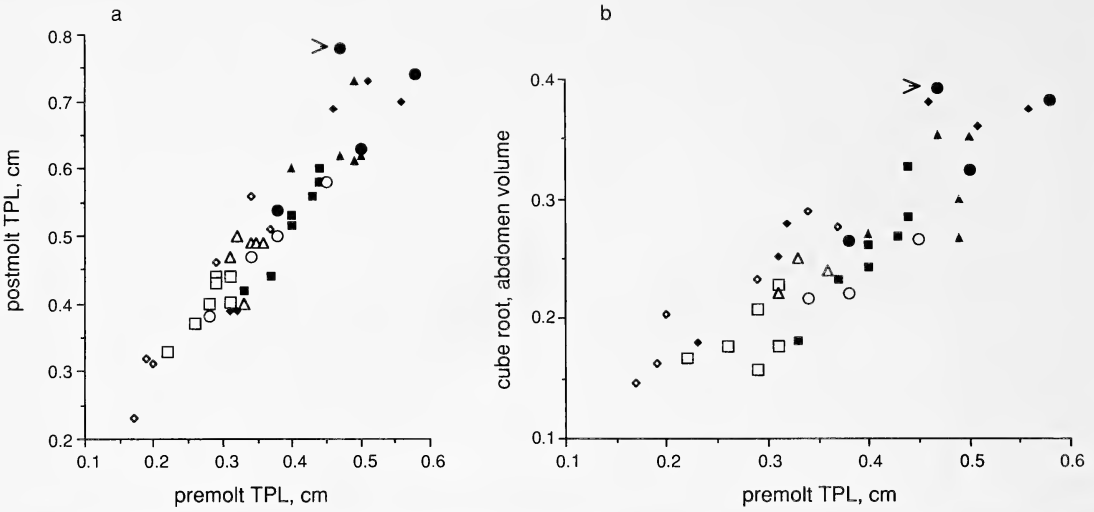

Figure 5.—Growth in the laboratory by spiders from four populations. Data from two molts are plotted, with the first molt indicated by open symbols and the second indicated by closed symbols. Squares = Chamela; diamonds = Tehuacán; triangles = Fortín; circles = Nanciyaga. The arrows indicate values for the male from Nanciyaga that delayed molting. Graph *a* = Growth per ecdysis in the laboratory, plotted as postmolt TPL (leg I tibia + patella length) *vs.* premolt TPL. Graph *b* = Premolt abdomen volume as a function of premolt TPL.

Common garden experiment.—Twenty-three spiders with TPL of 0.2–0.4 cm were brought to the laboratory from Nanciyaga, Fortín, Tehuacán, and Chamela and held for one complete intermolt cycle (two molts). The entire study lasted from June to October, and while all changes in TPL were verified by myself, variation caused by different persons making measurements produced increased error in the estimations of abdomen volume. In particular, data from two dates had to be excluded from the analysis of increasing abdomen volume, resulting in removal of five observations.

A total of 13 males were included in the study and five of them molted to maturity in the second molt in the laboratory: one from Nanciyaga, two from Fortín and two from Tehuacán. Therefore, analyses included the parameter of juvenile *vs.* maturation molt where appropriate.

Utilizing both observed molts for each individual, regression analysis of growth per ecdysis was significant for each population (all $P < 0.003$) (Fig. 5a). ANCOVA of growth per ecdysis showed no significant difference among these populations or between juvenile and maturation molts (no interaction effects, $P > 0.1$; ANCOVA. TPL: $F_{(1, 38)} = 230.9$, $P < 0.001$; population: $F_{(3, 38)} = 0.55$, *ns*; maturation: $F_{(1, 38)} = 0.004$, *ns*). These data were compared to 37 observations of molts in the field from the same sites and the same premolt TPL (0.2–0.5 cm). Preliminary analysis revealed no significant difference in slope among sites or between conditions (field or laboratory), nor a significant interaction of site and condition (ANCOVA: site × TPL: $F_{(3, 68)} = 0.43$, *ns*; condition × TPL: $F_{(1, 68)} = 0.10$, *ns*; site × condition: $F_{(3, 68)} = 0.14$, *ns*). Final ANCOVA testing for primary effects showed no significant variation due to site or condition (TPL: $F_{(1, 75)} = 450.9$, $P < 0.001$; site: $F_{(3, 75)} = 1.52$, *ns*; condition: $F_{(1, 75)} = 0.65$, *ns*).

Several parameters describing the intermolt interval were collected from the laboratory animals (Table 4). ANOVA showed no significant difference among populations in mean TPL following the first molt in the laboratory, although Nanciyaga and Fortín individuals were slightly larger. The total intermolt interval and the number of days foraging between molts were not affected by these slight differences in size (regression of total intermolt duration: TPL: $F_{(1, 15)} = 1.35$, *ns*; regression of days foraging: TPL: $F_{(1, 14)} = 3.43$, *ns*). The total intermolt interval and days foraging in the laboratory varied among sites but was not affected by whether the individual molted to sexual maturity (ANOVA of intermolt interval. site: $F_{(3, 16)} = 3.69$, $P = 0.03$; maturity: $F_{(1, 16)} = 1.64$, *ns*; ANOVA of days foraging. site: $F_{(3, 15)} = 4.69$, $P = 0.02$; maturity: $F_{(1, 15)} = 0.002$, *ns*). Differences between Nanciyaga and the re-

Table 4.—Intermolt duration in the laboratory for spiders from four populations. The TPL (leg 1 tibia + patella length) reported is the measurement following the first molt in the laboratory. Letters refer to statistically similar values among sites.

Site	*n*	TPL ± 1 SD	Total days ± 1 SD	Days foraging ± 1 SD
Nanciyaga	4	0.48 ± 0.08	26.8 ± 8.0 (a)	24.3 ± 9.0 (c)
Fortín de las Flores	6	0.47 ± 0.04	18.8 ± 4.0 (b)	15.4 ± 2.5 (d)
Tehuacán	6	0.40 ± 0.13	17.3 ± 4.3 (b)	14.8 ± 3.9 (d)
Chamela	7	0.40 ± 0.04	18.7 ± 3.1 (b)	13.2 ± 1.7 (d)

maining sites appear due to one male from Nanciyaga that took over 30 days to complete the intermolt interval and molt to maturity, twice the usual intermolt duration for spiders of this size.

The abdomen volume gain in the laboratory was independent of site. In the first molt, spiders from Tehuacán molted at a significantly higher premolt abdomen volume (no interaction affects; ANCOVA. site: $F_{(3, 13)} = 5.42$, $P = 0.01$). All spiders molted at the same relative abdomen volume in the second molt (no interaction affects; ANCOVA. TPL: $F_{(1, 16)} = 43.4$, $P < 0.001$; site: $F_{(3, 16)} = 2.61$, *ns*; maturity: $F_{(1, 16)} = 1.3$; *ns*) (Fig. 5b). Because there was no difference in the second molt in premolt abdomen volume among sites or between molts to maturity and juvenile molts, data from all individuals held for a complete intermolt cycle (including three of unknown origin) were combined to describe the pattern of abdomen volume increase over the intermolt. The relative change in abdomen volume [ln(av(d)/av (0)], where d = day and 0 = day of molt, was plotted against time for spiders molting within 20 days, for spiders molting in 20–26 days, and for the individual from Nanciyaga requiring 36 days (Fig. 6). The general trend was for the rate of abdomen volume increase to slow as the spiders approached the next molt. The individual from Nanciyaga that took longer between molts did achieve a greater premolt abdomen volume and grew slightly more at ecdysis than the other spiders, as indicated in Figs. 5a and 5b by arrows.

DISCUSSION

In order to interpret variation in phenology and size at maturity, the proximal developmental causes of the variation must be identified. In arthropods, variation in two developmental parameters can lead to differences in size at maturity: there may be variation in the change in size at each molt, or there may be variation in the number of juvenile molts. Variation in either parameter can result in the same adult size, but the conditions under which each varies may be distinct. Genetic variation or phenotypic plasticity can lead to differences in development within and among populations, but the evolutionary consequences of each source of variation are distinct (Pease & Bull 1988). Longitudinal observations of juvenile growth are a first step towards determining how environmental factors generate differences in adult size, and whether these differences are the result of phenotypic response to the environment or genetic variation among individuals within or among habitats. The results of the studies of *N. clavipes* imply that some developmental parameters are highly plastic while growth per ecdysis is constrained and may be genetically determined (Higgins 1992a, present study). Such information is not available from the census data presented in past arachnological studies without making basic assumptions concerning developmental processes.

Traditionally, field measures of growth utilized either frequency distributions of a single measure, such as carapace width, or the regression of two allometric body parts of individuals. The difficulties of determining growth and instar number from the former measure have been recognized (Polis & Sisson 1990); however, the latter analysis also presents incomplete information (Teissier 1960). In his formulation $dx/dt = \alpha Gx$, Huxley assumes constant growth per unit time if the environmental factors represented by G are constant (1972, p. 6). In order to determine the rate of growth or the growth per ecdysis (t = 1 instar), one must assume that the individuals are moving along the trajectory described by the allometric relationships at a constant rate of growth per ecdysis, an assumption that may be invalid if the growth per ecdysis responds to environmental factors (G). This assumption is invalid for the linyphiid *Linyphia triangularis* Clerck and may be invalid for the lycosid *Lycosa helluo* (Turnbull 1962, Uetz et al. 1992). Turn-

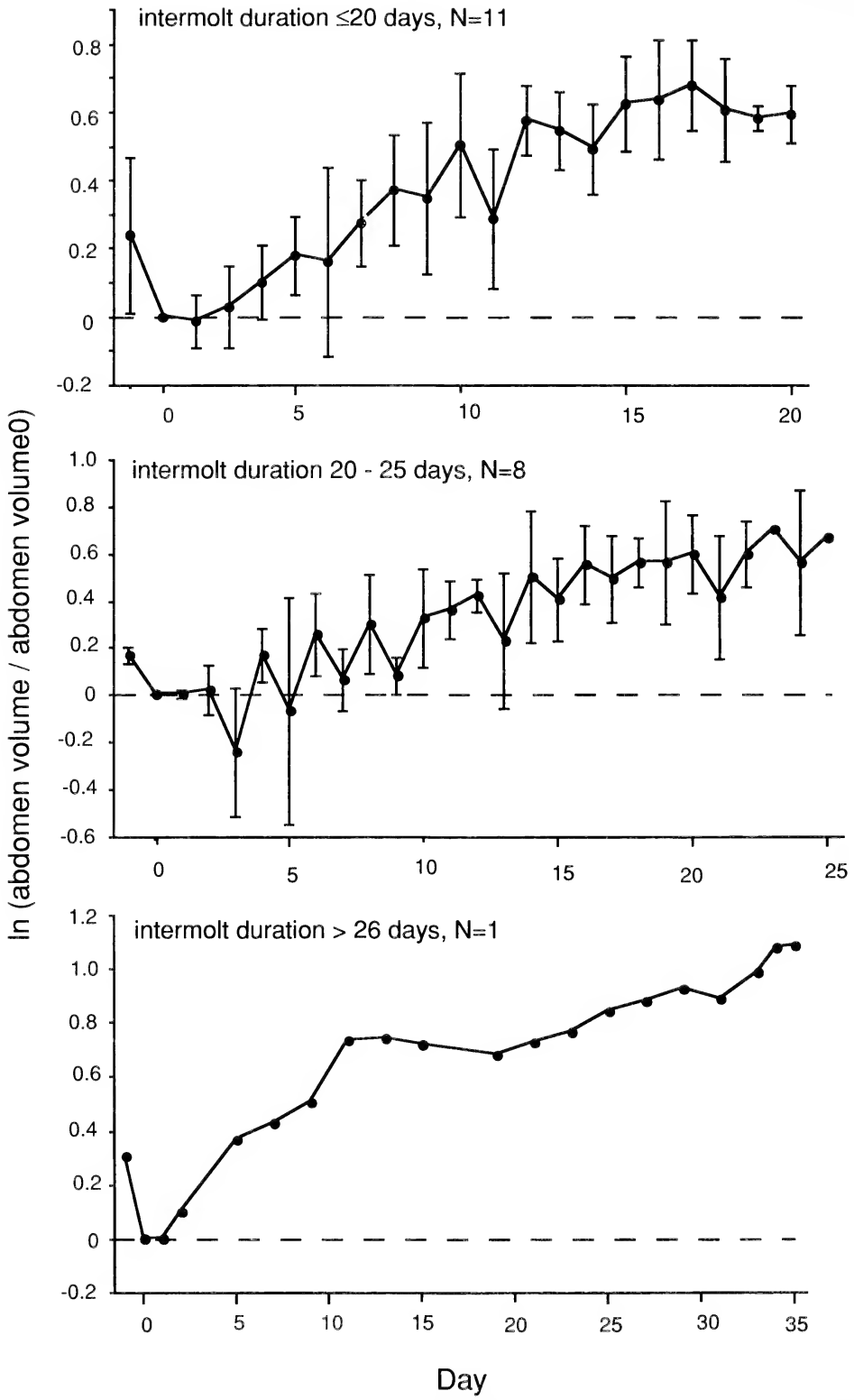

Figure 6.—Mean and SD of abdomen volume gain in the laboratory over time. Spiders from all sites were grouped according to the duration of the intermolt.

bull (1962) found that juvenile *L. triangularis* raised on quantitatively different diets molted at distinct, diet-dependent premolt weights. Implicit in his data is that the spiders grew different amounts in ecdysis, and due to this variation achieved different sizes at sexual maturity. He apparently did not observe variation in the number of juvenile instars. Uetz et al. (1992) found that sibling groups of *L. helluo* reared to maturity on qualitatively different diets varied in age and size at maturity as well as in juvenile mortality. It is unknown what developmental parameter varied with diet. Variation in the number of juvenile instars has been found for spiders in diverse families (Levi 1970), but the relative importance of variation in growth per ecdysis and variation in the number of juvenile instars in determining final adult size is unclear in previous studies of spiders (Levi 1970, Edgar 1971, Miyashita 1986, Wise 1987). Strikingly, despite the temporal variation in food levels experienced by many spiders (Riechert & Luczak 1982, Higgins & Buskirk 1992), there is as yet no evidence in spiders of the retrogressive or supernumary molts characteristic of many holometabolous insects subjected to poor diets or starvation (e. g., Beck 1972, Nijhout & Williams 1974). However, allometric data collected without longitudinal studies would not detect such molts if they did occur.

In *N. clavipes,* there is surprisingly little variation in the developmental trajectory described by growth per ecdysis. The data from field and laboratory reinforce the previous data, revealing stronger constraints in growth per ecdysis than previously reported (Higgins 1992a). Only the smallest individuals showed variation in growth per ecdysis, whereas larger juveniles and penultimate-instar individuals molt at the minimum premolt weight. I postulate that this shift from variable to constant growth per ecdysis may reflect either the reduction in predation pressure with increased size of the spiders or changes in the benefit of delayed ecdysis.

Growth per ecdysis in this spider is highly correlated with the premolt abdomen volume, and the premolt abdomen volume is size-specific and does not vary among the Mexican populations. Spiders from the isolated, desert population at Tehuacán might be expected to differ in their development, as they experience a short growing season and low rainfall (Higgins pers. obs.). In fact, the slope of growth per ecdysis appears to be lower in Tehuacán (Table 3) and is the same as that reported for the Texas, USA, population (Higgins 1992a). However, perhaps due to the small sample size from Tehuacán, the slope of growth per ecdysis did not differ statistically from the other five Mexican sites. Among these five sites, there is no apparent or statistical difference in growth per ecdysis, and these developmental trajectories are equal to those observed in Panama and in another coastal Veracruz site, Los Tuxtlas. Although I previously predicted that the spiders under good conditions (such as warm, moist coastal Veracruz) might accelerate development by delaying each molt, surpassing the minimum premolt abdomen volume and growing more at the next ecdysis (Higgins 1992a), this was observed only for spiders in the earliest instars. These small spiders are in the most heavily predated size class (Higgins 1992b) and may be seeking to escape predation by rapidly increasing their size (Wilbur & Collins 1973). Growth per ecdysis declines and is less variable after the spiders reach 0.3 cm TPL.

The shifts from variable to constant growth per ecdysis could also reflect the allometric relationship of postmolt TPL and premolt abdomen volume, described by a concave curve. For very small spiders, slight changes in premolt abdomen volume greatly alter postmolt TPL, so small delays in molting accompanied by weight gain will have a large effect on growth. For larger juveniles, small changes in abdomen volume have little effect on postmolt TPL, so much longer delays in molting are required for a significant change in growth in ecdysis. This is seen in the very slight increase in growth per molt for the individual from Nanciyaga that delayed molting during the common-garden experiment. This reduced benefit of delayed ecdysis could also explain the patterns seen in animals molting to maturity, which are of sizes found on the asymptote of the curve.

Spiders in the penultimate instar have partially developed external genitalia and are committed to becoming sexually mature in the next instar. Therefore, delaying maturity through additional juvenile molts is not an option. Males and females molting to sexual maturity molt at lower relative premolt abdomen volumes than juveniles molting to a juvenile instar. This is presumably due to the high benefit of reaching sexual maturity early compared to the slight increase in size that may be achieved by delayed ecdysis in the last instar. Both male and female reproductive success increase with increased adult size

(Christenson & Goist 1979, Vollrath 1980, Higgins 1992a), but the importance of early maturation is known only for females. Females maturing earlier in seasonal environments have greater likelihood of reproducing and greater likelihood of producing several egg sacs than do females maturing later (Higgins pers. obs.). There is an increase in fecundity per egg sac with increased TPL (Higgins 1992a), but increasing the number of egg sacs is proportionally more important as each egg sac may contain over 1000 eggs.

Although *N. clavipes* exhibits wide variation in size at sexual maturity, the developmental trajectory of this species described by growth per ecdysis is apparently highly constrained within a population and may be genetically determined. The spiders must achieve a given minimum premolt weight (here presented as premolt abdomen volume) prior to molting, and most spiders molt soon after reaching this weight. Premolt weight is size-dependent and independent of diet either in the field (current study) or in the laboratory (Higgins pers. obs.). That it is possible for the spiders to surpass the minimum premolt weight is apparent from the growth patterns of the smallest juveniles, and from occasional observations of spiders in the laboratory that surpass the minimum weight and grow more in the subsequent molt (present study; Higgins pers. obs.). This may reflect either phenotypic plasticity or genetic variability in minimum premolt weight. If phenotypic plasticity exists for premolt weight, it is rarely expressed after the fourth instar. If we assume that the selection has operated to optimize the developmental trajectory, these data indicate that, during the later juvenile instars, the costs of delayed molting outweigh the benefits of increased growth per ecdysis. This may be particularly true if, as implied by the concave relationship between premolt weight and postmolt size, increasingly long delays are required for significant differences in growth. However, the physiological and ecological costs of molting are not well enough understood to describe this optimization function, and the presence of specific constraints in premolt conditions must be determined first. Only future studies of the physiological and genetic controls of ecdysis in spiders will clarify this optimization function.

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PATHOGENS AND PARASITES OF OPILIONES (ARTHROPODA: ARACHNIDA)

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ABSTRACT. This is the first paper to review the literature records on all pathogens and parasites of Opiliones on a global level. These organisms (bacteria, fungi, protozoans, cestodes, trematodes, nematodes, arthropods) are listed in phylogenetic order along with available information on hosts, collection localities, life history, and taxonomic history. The opilion hosts are also listed (by their currently accepted names) along with the names of their known pathogens and parasites. Diagnostic characters and some taxonomic keys are provided for taxa which are relatively well know. Citations to other available keys are provided. Many new host and distribution records are provided.

Two fungi [*Engyodontium aranearum* (Cavara), *Torrubiella pulvinata* Mains] are removed from the list of pathogens of opilions and it is suggested that the original hosts were misidentified spiders.

Two new combinations are recorded in the Mermithidae: *Agamomermis phalangii* (Haldeman 1851), *Agamomermis truncatula* (Rudolphi 1819). *Agamermis incerta* Steiner in Stipperger 1928 is regarded as a *nomen nudum*.

The type locality of the mite *Leptus lomani* (Oudemans 1903b) is restricted to Corral (39°53'S, 73°25'W), Valdivia, Chile.

Unlike many arachnids, Opiliones or harvestmen lack a pumping stomach and therefore they chew their food and often consume oocysts and spores. Examination of their feces reveals a variety of chitinous fragments from their arthropod prey as well as plant pieces. Some saprophytic fungi and yeast spores can be observed as well as gametocytes of internal parasites. The frequent grooming of the legs by the harvestmen may also lead to the ingestion of oocysts and spores. While ingestion is the common entrance pathway for some opilion pathogens, fungi infect their host through penetration of the cuticle. Although gregarines and mites are frequently encountered when observing harvestmen, relatively few researchers have documented their occurrences.

Harvestmen are unique among arthropods by possessing bilateral exocrine glands which open onto the dorsal surface of the cephalothorax near the base of the second pair of legs. These glands produce a variety of volatile secretions (Ekpa *et al.* 1984, 1985) that have been generally considered to be defensive in nature. The glands have also been proposed to function in a variety of other behaviors including protection from external pathogens and parasites (see Holmberg 1986, and citations therein). To date, only defense against predators and harvestman aggregation formation have been demonstrated.

While working with a South America harvestman, Estable *et al.* (1955) discovered that the exocrine gland secretion was a remarkably effective antibiotic, *in vitro*, against 18 genera of bacteria (Gram positive and negative) and protozoa. Their work revealed that the secretion was also active when given orally to mice infected with intestinal parasites. The substance was tolerated perfectly by the mice but destroyed giardias, trichomonas and hexamites. The components of the secretion were later determined to be a composed of a variety of quinones (Fieser & Ardao 1956).

The major components of the exocrine secretions of harvestmen differ between the two suborders, Laniatores and Cyphopalpatores. Minor components and ratios of components differ among congeneric species (Ekpa *et al.* 1985). The few chemical analyses thus far reported (see Ekpa *et al.* 1984, and citations therein) from Laniatores reveal a variety of alkylated benzoquinones, phenols, N,N-dimethyl-β-phenylethylamine and bornyl esters. Only the Palpatores section of the suborder Cyphopalpatores has been chemically investigated. Those analyses reveal

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members of this group secrete short-chained acyclic ketones, alcohols and naphthoquinones (see Ekpa *et al.* 1985, and citations therein).

Even though harvestmen are abundant in warm moist situations, few records are available of fungi infecting these animals. Because the major components of harvestman exocrine secretions are members of chemical classes known to be fungicides (see Torgeson 1969; Cole *et al.* 1975), it is likely these secretions are used to protect harvestmen from infection. The use of these secretions in defense and grooming needs further study.

While there are several world-wide taxonomic revisions of harvestmen, no similar treatment for their parasites has been undertaken. This is in part due to the incorrect view that harvestmen are not of economic importance. Mounting evidence demonstrates that harvestmen are beneficial and that they consume considerable quantities of pest insects and mites. Because of this beneficial status, no one has investigated parasites for controlling opilions. Experiments involving insect pathogens on harvestmen reveal opilions are susceptible. Like conventional insecticides, insect pathogens and parasites could have a severe impact on the beneficial harvestmen.

Many of the records of parasites from harvestmen are incomplete. In some cases the host, but not the parasite, is identified to species. In other cases, the parasite but not the host is identified to species. The purpose of this contribution is to bring together the limited information on this topic so that a foundation can be built for future research.

Because of the lack of good characters in some groups (*i. e.*, Microsporida and juveniles of Mermithidae) collective groups have been named. Such groups or genera often include species which probably are not related. This group name is used simply for "taxonomic convenience" and includes species not readily placed in known genera (possibly because a particular life stage is unknown) and species *incertae sedis*. Some taxonomically convenient groups also occur at higher levels in fungi. In fungi, the sexual stage (teleomorph of ascomycetes and basidiomycetes) and their asexual stages (anamorphs or conidial stages) are sometimes placed in separate genera and classes. In some cases, two or more ascomycetes may be identified as having the same form species for an anamorph.

When one discusses parasites of opilions, the topic of phoresy arises. Phoresy is not parasitism but rather a form of symbiotic relationship in which the smaller organism associates with the harvestman in order to obtain transportation. Phoresy as well as passive transport of fungal and plant spores will not be examined here.

Superkingdom Prokaryotae
Kingdom Monera
Division Gracilicutes
Family Enterobacteriaceae

Xenorhabdus Thomas & Poinar contains five described species and other undescribed species (Akhurst & Boemare 1990). They typically inhabit nematodes and their host arthropods (insects and arachnids). See under Nematoda (Rhabditoidea) for further details on this relationship. Pertinent taxonomic papers are cited with a review of the taxonomic problems in Akhurst & Boemare (1990).

Xenorhabdus luminescens Thomas & Poinar (1979) is introduced into the arthropod host by a Heterorhabditidae [*Heterorhabditis bacteriophora* Poinar]. Poinar & Thomas (1985) demonstrated this bacterium could kill a Phalangiidae (*Phalangium opilio* Linn., reported as *P.* sp.) if introduced by the correct nematode.

Xenorhabdus nematophilus (Poinar & Thomas 1965) was originally described in combination with *Achromobacter* Bergey, Breed & Murray. This bacterium is introduced into the arthropod host by a Steinernematidae [*Steinernema carpocapsae* (Weiser)]. Poinar & Thomas (1985) demonstrated that this bacterium could kill a Phalangiidae, *Phalangium opilio* (reported as *P.* sp.), if introduced by the proper nematode.

Superkingdom Eukaryotae
Kingdom Fungi
Division Eumycota

At least one species of fungus successfully kills a Gonyleptidae (see under *Torrubiella gonylepticida* and unidentified fungi). Gonyleptoidea are known to have phenols which are antagonistic to fungal growth in their exocrine secretions. Either *T. gonylepticida* and another unidentified fungus from Panama are not retarded by phenols, or the hosts were unable to produce phenols in sufficient quantity. The extent of phenol production in various gonyleptid genera and its use in controlling fungi have not been investigated. Likewise, the effects of age and health of the har-

vestman on phenol production have not been examined.

Unidentified Fungi

Griffiths (1978) illustrated a harvestman [not identified, but almost certainly *Nelima paessleri* (Roewer)] covered by mycelia of soil microfungi. The fungi are reported not to be pathogenic, but simply use the harvestman corpse as a substrate.

Mora (1987, fig. 8) reported mortality in adult males of a Gonyleptidae (*Zygopachylus albomarginis* Chamberlin) by an unidentified fungus on Barro Colorado Island, Panama. Males of this nest-building harvestman eat all fungus appearing in the nest, thus preventing the proliferation of mycelia. Mora (1987) suggested the males ingested the fungi (spores) which eventually killed them. This is probably incorrect because nearly all other fungal pathogens of invertebrates infect their host through the cuticle (Samson *et al.* 1988). Ten fatalities were observed from 199 nest-guarding males examined by Mora.

Subdivision Ascomycotina
Class Pyrenomycetes
Order Clavicipitales
Family Clavicitaceae

Torrubiella Boudier is a genus with primary host affinities for spiders (Araneae), although several species are also known from insects, especially Coccidae (Kobayasi & Shimizu 1982; Humber & Rombach 1987). Two species have been reported from harvestmen, but only one report appears to be valid.

Torrubiella gonylepticida (Möller 1901) was originally described in combination with *Cordyceps* Fries. Petch (1937) transferred the species to its present combination and redescribed the species. Möller (1901), when describing the host, referred to it as a spider ('Die Spinnen', not 'Weberknechte'). Subsequent authors (Petch 1937; Koval 1974; Kobayasi & Shimizu 1982) have continued to list the only host as a spider. Fortunately, the specific name refers to the true type host, a Gonyleptidae harvestman. Möller (1901, taf. 6, fig. 89) clearly illustrated the gonyleptid host, but not in sufficient detail to determine to which genus it belongs. Kobayasi & Shimizu (1982) reprinted Möller's illustration and stated the type locality was Brazil.

Petch (1937) described the conidial stage as *Spicaria longipes*; which is now recognized as *Paecilomyces farinosus* (Holm *ex* S. F. Gray) (Brown & Smith 1957). Petch recorded *T. gonylepticida* and the conidial stage from various spiders from Trinidad. Koval' (1974) listed the conidial stage from spiders collected on *Magnolia* Linné leaves in Russia (formerly Russian Soviet Federative Socialist Republic, USSR). In the key to *Torrubiella* spp. by Koval', two varieties of *T. gonylepticida* are differentiated on the basis of perithecia and ascus lengths. However, the two taxa should be attributed to another species: the third taxa in the key should be *T. arachnophila* var. *pleiopus* Mains and the fourth should be *T. arachnophila* var. *pulchra* Mains.

Torrubiella pulvinata Mains (1949) was described from "Opilionoidea" collected on Oahu, Hawaii. *Paecilomyces* (reported as *Spicaria*) *pulvinata* (Mains 1949) was the name given to the conidial stage. Samson (1974) listed *S. pulvinata* as a synonym of *P. farinosus*, thus regarding the anamorph for both *T. gonylepticida* and *T. pulvinata* to be the same species. Mains (1949, p. 303) stated "The hosts of this collection are so severely parasitized that accurate determination is difficult. They appear to be arachnids belonging to the Opilionoidea." Because opilions appear to be absent from the Hawaiian Islands (F. G. Howarth pers. commun.), the host is more likely a long-legged, pholcid spider. The setae-spines on the legs illustrated by Mains (1949, fig. 1A) are long and unlike those on harvestmen. They are similar to those found on spiders. There are five adventive cosmopolitan Pholcidae (Araneae) established in the islands that could be confused as opilions by non-specialists. The opilion host records are considered here to be incorrect.

Subdivision Deuteromycotina
Class Hyphomycetes

The Hyphomycetes is an artificial class representing the asexual states of Ascomycetes and Basidiomycetes, or fungi for which sexual states are unknown. Orders and families do not exist in current classifications of these fungi.

Hymenostilbe Petch is comprised of seven described species. Species are known to infect a variety of insect hosts, spiders (Mains 1950; Evans & Samson 1987) and harvestmen. Mains (1950) stated members of this genus are the conidial (anamorph) state of *Cordyceps* spp.; whereas

Evans & Samson (1987) reported the teleomorph connection remains unproven. Specific identifications are best made by consulting the diagnoses provided by Mains (1950). *Hymenostilbe verrucosa* Mains (1950) was originally described from spiders collected in Maine, USA. Other records are from spiders in England and a "Phalangiidae" in England (Leatherdale 1970).

Engyodontium de Hoog is comprised of seven species, two of which are reported to infect spiders and one on "opilionids". A key to the species is provided by Gams *et al.* 1984. *Engyodontium aranearum* (Cavara) was originally described in the genus *Sporotrichum* Link *ex* Fries and was transferred to its present combination by Gams *et al.* (1984). A redescription and synonymy are provided by Gams *et al.* (1984). The teleomorph state is unknown, but other members of the genus have a *Torrubiella* teleomorph. Those same authors reported hosts as a fly, spiders and opilions. The specimen in their photograph (fig. 3), as well as those of Samson *et al.* (1988, pl. 68a,b), superficially resembles opilions, but judging from the dense placement and morphology of the setae on the host legs (figs. 3, 68b) they are not harvestmen. They are more likely pholcid spiders (Araneae: Pholcidae). The opilion host record for this species of fungus is considered herein incorrect.

Nomuraea Maublanc is composed of three described species (Ignoffo *et al.* 1989; Greenstone *et al.* 1988). *Nomuraea rileyi* (Farlow) Samson is a well-known pathogen of insects. *Nomuraea atypicola* (Yasudo) Samson is reported to infect spiders, harvestmen and insects. *Nomuraea anemonoides* Hocking was originally isolated from soil and, in high doses in the laboratory, can cause mortality in insects.

Nomuraea atypicola (Yasuda 1915) was originally described as a member of the genus *Isaria* J. Hill *ex* E. M. Fries. It was found on an Atypidae spider in Japan. It was transferred to its present combination by Samson (1974). The teleomorph or sexual state is *Cordyceps cylindrica* Petch (1937). Greenstone *et al.* (1988) reported the infection of a harvestmen by this fungus under laboratory conditions. The infected Sclerosomatidae, *Leiobunum vittatum* (Say), was collected in Missouri, USA. This species of fungus is commonly found infecting spiders (Greenstone *et al.* 1988) and under laboratory conditions was also found to be infective to Lepidoptera larvae (Ignoffo *et al.* 1989).

Subdivision Zygomycotina
Class Zygomycetes
Order Entomophthorales
Family Entomophthoraceae

Pandora Humber (1989) is comprised of 16 species of obligately pathogenic fungi. Hosts include members of insects and arachnids. A single species is recorded from opilions. *Pandora phalangicida* (Lagerheim 1898) was originally described from Phalangiidae collected in Sweden as a species of *Empusa* Cohn (*Entomophthora*). Batko (1966) transferred the species to *Zoophthora* Batko 1964, and placed it in the subgenus *Pandora* Batko 1966. Humber (1989) placed it in his new genus *Pandora*. Ellis (1956) and Leatherdale (1958, 1970) recorded this fungus from a Phalangiidae, *Phalangium opilio*, in England.

Entomophaga Batko includes 10 described species (Humber 1989). All are obligate pathogens of insects and arachnids. A single species is recorded from opilions. A key for identification of members of this genus is provided by Keller (1987). Comparisons to original descriptions (species and citations are listed in Humber 1989) are required for positive identifications. *Entomophaga batkoi* (Bałazy 1978) was originally described in the genus *Entomophthora* Fresenius. Later, Remaudière & Keller (1980) transferred the species to *Conidiobolus* Brefeld (Family Ancylistaceae), but the current combination with *Entomophaga* was made by Keller (1987). Bałazy (1978) described this fungus from harvestmen collected near Poznań, Poland. Phalangiidae [*Oligolophus tridens* (C. L. Koch)] and rarely Sclerosomatidae (*Leiobunum rotundum* Latreille and *Leiobunum blackwalli* Meade) were infected. An epizootic (temporary increase in the incidence of infections) was observed during late summer.

Keller (1987) reported this species of fungus was rather common and often caused epizootics in open woods, along the borders of forests and hedges. From late July to the middle of September it was collected from *Oligolophus tridens* in Switzerland.

Kingdom Animalia
Subkingdom Protozoa

Although seldom reported, Protozoa are common parasites of Opiliones. To date, all records of Protozoan parasites of Opiliones are from USA,

Europe and India. Their reported absence from other localities is likely due to lack of study. While dissecting gonads for anatomical and chromosomal studies, I have often observed gregarines from North and Middle America species (especially from Phalangiidae and Cosmetidae). Ellis (1913, p. 280) reported that he was unable to locate gregarines in the "alimentary canal of perhaps two hundred Phalangidea" from Michigan and Colorado. His failure to locate parasites may have been caused by the time of year he examined the opilions or possibly the taxa he examined do not harbor gregarines (these taxa are unknown, but probably are members of the Sclerosomatidae: Leiobuninae as they are the dominate forms in the two mentioned areas). Only two studies have been published on opilion hematocytes, one of which resulted in the discovery of a blood parasite.

Phylum Microspora
Class Microsporea
Order Microsporida
Collective Group *Microsporidium*

Species that cannot be readily placed to genus, as well as species *incertae sedis*, are lumped into *Microsporidium* sensu Sprague (1977). *Microsporidium weiseri* (Šilhavý 1960) was originally described in the genus *Stempellia* Léger & Hesse (Family Thelohaniidae). Sprague (1977) transferred this species to its present combination with *Microsporidium* because the species did not fit any of the known genera. This parasite was found in smear-preparations of hemolymph of a Phalangiidae, *Opilio parietinus* (De Geer). The harvestmen was collected in Třebíč, Czechoslovakia. The plasmodium have 2, 4, 8 and 16 spores and are found in the hemolymph and hemocytes (plasmatocytes) of its host.

Phylum Apicomplexa

All known Apicomplexa parasites of opilions are septate eugregarines and as such have several features in common. Both sexual and asexual stages occur (gametogony and sporogony), but merogony is absent. The mode of infection is ingestion of oocysts. The trophozoites attach to the lining of the gut and divide to form merozoites and gamonts. Gametocytes are passed in the feces, and no intermediate host or vector is needed. Because most species are believed to attach to intestinal epithelial cells, gregarines in opilions probably are not pathogenic.

The gregarine genera and some species known from harvestmen can be identified by the following taxonomical key. Because some species are inadequately described (some life-stages unknown) identifications to species are difficult. Useful keys or tables of characters are mentioned under specific genera in the following account.

Class Sporozoasida
Subclass Gregarinasina

Tsurusaki (1986) found gregarines in Sclerosomatidae harvestmen, *Leiobunum manubriatum* Karsch and *Leiobunum globosum* Suzuki, from numerous localities in Japan. He also provided data on parasitism rates as related to species, locality and season. His gregarines have not been identified.

Hunt (1979) found numerous gregarines in the midgut diverticula of Triaenonychidae harvestmen, *Equitius doriae* Simon, from southeastern Australia. His gregarines were never identified.

Mitov reported (pers. commun.) that he had discovered gregarines in preserved material of the following harvestmen from Vitosha Mountain and West Rodopy, Bulgaria: Nemastomatidae [*Carinostoma ornatum* (Hadži), *Paranemastoma radewi* (Roewer), *Pyza bosnica* (Roewer)]; Sclerosomatidae [Leiobunum rumelicum Šilhavý]; Phalangiidae [*Lacinius ephippiatus* (C. L. Koch), *L. horridus* (Panzer), *L. dentiger* (C. L. Koch), *Lophopilio palpinalis* (Herbst), *Mitopus morio* (Fabricius), *Odiellus lendli* (Sørensen), *Opilio dinaricus* Šilhavý, *O. ruzickai* Šilhavý, *O. saxatilis* (C. L. Koch), *Phalangium opilio, Zacheus anatolicus* (Kulczyński), *Z. crista* (Brullé)].

Other new records include unidentified gregarines from a Phalangiidae, *Odiellus pictus* Wood, collected in the West Virginia University Forest, Chestnut Ridge, Preston County, West Virginia, USA and an unidentified gregarine from a Sclerosomatidae, *Leiobunum politum* Weed, collected in Columbus, Ohio, USA. This latter series is remarkable as the parasites were only discovered after a hundred years of storage.

Key For Identification Of Gregarines Found In Harvestmen

1a. Oocysts without spines or thickening at poles 2
1b. Oocysts with spines or thickenings at poles, sometimes at equator and also along edges ..... (Family Actinocephalidae) 5

Subfamily Acanthosporinae

2a. Epimerite simple, spherical; oocysts biconical, with truncate ends, released unchained by simple dehiscense of the gametocyst ..... Family Hirmocystidae
Arachnocystis arachnoidea (Devdhar & Gourishankar)

2b. Epimerite complex and varied; oocysts biconical orcylindroconical, united as a string of beads ..... Family Actinocephalidae 3

Subfamily Actinocephalinae

3a. Epimerite sessile, with short neck having 8–10 simple digitform processes at apex; neck persists more or less in sporont, but digitform processes (tentacles) disappear; gametocysts dehisce by formation of hole in wall through which oocysts are extruded in a single thread; oocysts biconical or lemon-shaped ..... *Actinocephalus megabuni* Ormières & Baudoin

3b. Epimerite without digitform process at apex, gametocysts rupture by simple dehiscence 4

4a. Epimerite a large, flattened and fluted disk, oocysts ovoid to biconical, in lateral chains. . . *Anthorhynchus*
Anthorhynchus longispora Ormières & Baudoin
Anthorhynchus sophiae (Schneider)

4b. Epimerite a large flattened centrally indented papilla with crenulate border, lost early. Protomerite with numerous vertical laminations, broadening to an umbrella in the mature sporont, each costule curved to form a spine pointing backward; oocysts biconical or ovoid, united as a string of beads . . . . *Sciadiophora*
Sciadiophora caudata (Rössler)
Sciadiophora fissidens (Rössler)
Sciadiophora gagrellula Devdhar & Amoji
Sciadiophora geronowitschi (Johansen)
Sciadiophora phalangii (Léger)
Sciadiophora claviformis Ormières & Baudoin

5a. Epimerite a conical knob, dentated at the base with a series (about 20) of vertical lamelle. Oocysts cylindrical with pointed ends, a tuft of spines at each pole ..... *Contospora opalniae* Devdhar & Amoji

5b. Epimerite simple, globular, without ornamentation 6

6a. Oocysts barrel-shaped, asymmetrical, without terminal tufts, with two equatorial (lateral) thickenings on longitudinal cordons ..... *Doliospora*
Doliospora repelini (Léger)
Doliospora troguli (Geus)

6b. Oocysts biconical and symmetrical 7

7a. Oocysts with 8 to 10 slender spines at each pole and released in chains of 2 to 3 or more from the gametocyst ..... *Echinoocysta phalangii* (Amoji & Devdhar)

7b. Oocysts with slender spines on poles and sides; released unattached from the gametocyst ..... *Cosmetophilus vonones* Cokendolpher

Order Eugregarinorida
Suborder Septatorina
Superfamily Gregarinicae
Family Hirmocystidae

Arachnocystis Levine is restricted to Oribatei mite and opilion hosts. Four species are known, of which one (the type species) occurs in opilions (Levine 1979, 1985). *Arachnocystis arachnoidea* (Devdhar & Gourishankar 1971) was originally described in the genus *Sycia* Léger (Family Lecudinidae). Levine (1979) transferred the species to his new genus *Arachnocystis,* where it was designated the type species. This species was found in the intestinal ceca of an Assamidae, *Oppalnia* sp. (reported as *Opalnia* sp., see Cokendolpher 1991), from Someshwar near Dharwar, Karnataka State, India (Devdhar 1962).

Superfamily Stenophoricae
Family Actinocephalidae
Subfamily Actinocephalinae

Actinocephalus Stein is a relatively large genus with about 40 described species in insects and one in an opilion (Levine 1985). *Actinocephalus megabuni* Ormières & Baudoin (1973) was discovered in the intestine of a Phalangiidae, *Megabunus diadema* (Fabricius). It was collected in Besse, France.

Anthorhynchus Labbé are found in a termite (Kalavati & Narasimhamurti 1978) and opilion hosts. Two species are described from harvestmen. The type species, by monotypy, is *Anthorhynchus sophiae* Schneider; an opilion parasite.

Anthorhynchus longispora Ormières & Baudoin (1973) was described from the guts of two

families of harvestmen: Sclerosomatidae [*Leiobunum* (reported as *Liobunum*) *rotundum*] and Phalangiidae [*Mitopus morio*, *Opilio parietinus*, *Platybunus bucephalus* (C. L. Koch)]. All harvestmen were collected near Besse-en-Chandesse, France.

Anthorhynchus sophiae (Schneider 1887) was originally described in the genus *Anthocephalus* Schneider. Because that generic name is preoccupied, Labbé (1899) provided the replacement name and transferred the species to its present combination. The original collection of this parasite was from the intestine of a Phalangiidae, *Phalangium opilio*, captured in Poitiers, France. This species is also reported by Pfeifer (1956, from Germany) and Ormières & Baudoin (1973, from France) from the Sclerosomatidae [*Leiobunum blackwalli* (reported as *L. hassiae* Müller), *Leiobunum* (=*Liobunum*) *rotundum*] and the Phalangiidae [*Lacinius ephippiatus*, *Mitopus morio*, *Oligolophus tridens*, *Phalangium opilio*, *Rilaena* (reported as *Platybunus*) *triangularis* (Herbst)].

Sciadiophora Labbé are restricted to opilion hosts. There are five described species. Devdhar & Amoji (1978a) provided a table of characters which is useful in making identifications.

Sciadiophora caudata (Rössler 1882) was originally described in the genus *Stylorhynchus* Stein. Because that name was preoccupied, Ellis (1912) provided the new generic name *Stylocephalus*. Watson Kamm (1922) transferred the species to its present combination with *Sciadiophora*. This species was originally found in the intestines of Phalangiidae [*Mitopus morio*, *Odiellus* (reported as *Odius*) *spinosus* (Bosc), *Phalangium opilio*, Phalangiidae gen. sp.] from Germany. Ormières & Baudoin (1973) reported collections from the same three hosts from Besse and Tamarissière, France.

Sciadiophora fissidens (Rössler 1882) was first described in the genus *Actinocephalus* and was later transferred by Labbé (1899) to *Sciadiophora*. This species was found in intestines of Phalangiidae [*Lophopilio* (reported as *Odiellus*) *palpinalis*, *Phalangium opilio*, Phalangiidae gen. sp.] from Germany.

Sciadiophora gagrellula Devdhar & Amoji (1978b) was described from a Sclerosomatidae, *Gagrellula saddlana* (Roewer), which were collected in Dharwar and Kumta, Karnataka State, India (Devdhar 1962). This gregarine is found in the intestine and intestinal ceca. Unlike most described opilion parasites, this species is known (and illustrated) by all life stages.

Sciadiophora geronowitschi (Johansen 1894) was described in the genus *Actinocephalus* and was transferred to its present combination by Labbé (1899). This protozoa was discovered in the intestines of a Phalangiidae, *Phalangium opilio*, from Russia (formerly Russian Soviet Federative Socialist Republic, USSR).

Sciadiophora phalangii (Léger 1897) was first described in combination with *Lycosella* Léger. It was the type and only species in the genus. Because *Lycosella* was preoccupied, Labbé (1899) proposed the new name *Sciadiophora*, with *S. phalangii* being the type-species. This species has been recorded, redescribed and illustrated by numerous authors (Minchin 1903; Wellmer 1911; Ellis 1913; Watson Kamm 1922; Stipperger 1928; Pfeifer 1956; Šilhavý 1961; Geus 1969; Kudo 1971; Ormières & Baudoin 1973). Two families of harvestmen have been reported as hosts (all European): Sclerosomatidae [*Leiobunum rotundum*] and Phalangiidae [*Lacinius dentiger*, *Mitopus morio* (reported as *Opilio grossipes*), *Opilio parietinus*, *Phalangium* sp., *Phalangium opilio* (reported as *Phalangium cornutum*), *Platybunus bucephalus*, *Platybunus pinetorum* (C. L. Koch), *Rileana* (=*Platybunus*) *triangularis*]. The original collection of this species was recorded from two hosts, *Phalangium crassum* Dufour and *P. cornutum* from Vallée de la Loire (where it was rare) and Provence (where it was common), France. As noted above, the latter species is now known as *P. opilio* but the identification of the former species is uncertain (Roewer 1923). Records of this parasite are from France, Austria, Germany and Czechoslovakia.

Sciadiophora claviformis Ormières & Baudoin (1973) was found in the intestine of a Phalangiidae, *Mitopus* sp. (based on the collection locality the species is probably *M. morio*). The collection locality was Vallée de Chaudefour, France.

Subfamily Acanthosporinae

Contospora Devdhar & Amoji are known only from opilions. The single species, *Contospora opalniae* Devdhar & Amoji (1978a), was described from the midgut and cecum of an Assamidae, *Oppalnia* sp. (reported as *Opalnia* sp., see Cokendolpher 1991). It is known from Someshwar and Kalghatgi, Dharwar District, India (Devdhar 1962).

Cosmetophilus Cokendolpher is a monotypic genus restricted to an opilion host. It is the only genus of gregarines positively identified from harvestmen in the New World. *Cosmetophilus vonones* Cokendolpher (1991) was described from the intestine and intestinal ceca of the cosmetid harvestman *Vonones sayi* (Simon) from Texas, USA. Other samples presumably of this species were recorded from the same host collected in Tennessee, USA. Unlike most described opilion gregarines, this species is known (and illustrated) by all life stages.

Doliospora Ormières & Baudoin (1969) are restricted to opilion hosts. There are two described species. *Doliospora repelini* (Léger 1897) was originally described in the genus *Acanthospora* Léger (1892). It was designated the type-species of the new genus, *Doliospora*, by Ormières & Baudoin (1969). This species has been reported by Léger (1897) and Ormières & Baudoin (1973) from France from the intestines of the Sclerosomatidae [*Leiobunum* (=*Liobunum*) *rotundum*] and the Phalangiidae [*Oligolophus tridens*, *Opilio parietinus*, *Megabunus diadema*, *Mitopus morio* (=*O. grossipes*), *Phalangium opilio* (=*P. cornutum* - type host), *Platybunus bucephalus*].

Doliospora troguli (Geus 1969) was originally described in the genus *Acanthospora* and transferred to its current combination by Levine (1980). It was found in the intestine of a Troguloidae, *Trogulus tricarinatus* (Linné), in Rathsberg, Germany. Neither its gametocysts nor its oocysts are described.

Echinoocysta Levine (1984) is composed of a single species that is restricted to an opilion host. *Echinoocysta phalangii* (Amoji & Devdhar 1979) was originally described in the genus *Echinospora* Amoji & Devdhar (1979). Because that genus was preoccupied, Levine (1984) proposed the new name *Echinoocysta* and transferred the species to its current combination. This protozoa is found in the intestine and intestinal ceca of an Assamidae, *Oppalnia* sp. (reported as *Opalnia* sp., see Cokendolpher 1991) from Someshwar, near Dharwad, Karnataka State, India.

Subkingdom Eumetazoa
Phylum Platyhelminthes
Class Cestoda (Cestoidea)
Order Cyclophyllidea
Subclass Eucestoda
Family Hymenolepididae

Pseudhymenolepis Joyeux & Baer (1935) is monotypic. *Pseudhymenolepis redonica* Joyeux & Baer (1935) was described from the shrew *Crocidura russula* Herm. (Insectivora: Soricidae). A flea, *Ctenophtalmus arvernus* (Hystrichopsyllidae), is known to be an intermediate host of this cestode. Gabrion (1977) reported finding cysticercoides in a Phalangiidae, *Phalangium opilio*, collected during early July. The harvestman was found in a shrew nest (previously named species). Shrews in the general area of the nest revealed proglotids of this cestode as well. It has been proposed that *P. opilio* will serve as the intermediate host when fleas are absent.

Class Trematoda
Order Digenea

Creplin (1846, p. 156) reported finding an unidentified larval fluke in a Phalangiidae (*Phalangium opilio*). The fluke was listed as "*Distomum Cystidicola* Cr. sp. n." As no illustration or description was provided this name must be considered a *nomen nudum*.

Family Dicrocoeliidae

Brachylecithum Ström was originally described as a subgenus of *Lypersomum* Looss. Adult flukes of this genus are found in the liver and gall bladder of birds and rarely in mammals. Data are available on the life cycles of six (incomplete data for five species) *Brachylecithum* spp. (see Carney 1970, 1972). In a typical lifecycle the eggs are passed in the feces of the definitive host, a bird or mammal. The eggs are eaten by a terrestrial snail, the intermediate molluscan host, where they develop into miracidia and sporocysts. The cecariae emerge from the snail as a slime ball and are eaten by a second intermediate host (usually an arthropod). The cecariae encyst in the arthropod hemocoel and infect the vertebrate host upon eating the intermediate host. In some arthropod hosts, the metacercariae lodge in or near the host brain causing behavioral and morphological changes (Hohorst & Graefe 1961; Carney 1969). These changes appear to increase the chances of predation upon the arthropod host (Carney 1969).

Brachylecithum sp. cysts and metacercaires were reported from a Phalangiidae, *Phalangium opilio*, by Gabrion & Ormières (1973). The trematodes were found in the muscles and adipose tissue of the body. The infected harvestman was collected in Sète and Montpellier, France. *Brachylecithum* adults are known from Passeriformes birds in the south of France. Because *Brachlecithum* spp. appear to be relatively host-

specific in the arthropod stage of development (Carney 1970), the record in *Phalangium* is probably of an undescribed species.

Phylum Nematoda (Nemata)
Unidentified Class

Laniatores (Triaenonychidae and/or Synthetonychidae) from New Zealand are reported by Forster (1954) to be infested by unspecified nematodes. Dr. V. Tood (in Sankey 1949a) recorded nematodes from *Rilaena* (=*Platybunus*) *triangularis*.

Class Secernentia
Subclass Rhabditia
Order Rhabditida
Suborder Rhabditin
Superfamily Rhabditoidea
Family unidentified

Pfeifer (1956) reported "rhabditid" nematodes from Phalangiidae (*Lacinius horridus* and *Phalangium opilio*) that were captured in Berlin, Germany.

Family Steinernematidae

Steinernema Travassos is comprised of nine distinct species (Poinar 1990). Until recently, most species were referred to *Neoaplectana* Steiner. Others referred to *Neoaplectana* are either synonyms, misidentified or insufficiently described (Poinar & Welch 1981). Keys and other descriptive data needed for identification of the various species can be located in Poinar (1990). Only one species is known from a phalangid host. All species thus far discovered carry a single species of symbiotic bacterium in the alimentary tract of the third-stage juvenile. The infective stage nematodes occur on soil and have the ability to locate and enter arthropod hosts. To reach the hemolymph of the host, the nematodes enter via a natural opening and then penetrate through the gut or tracheal walls. Once inside the host, the nematode releases its associated bacterium which kills the host within 48 hours. The nematodes mature into males and females inside the arthropod and the females release eggs within the cadaver (Poinar 1983).

Steinernema carpocapsae (Weiser 1955) was originally described in combination with *Neoaplectana* from codling moth larvae collected in Czechoslovakia. Poinar & Thomas (1985) demonstrated this nematode could infect and successfully reproduce in a Phalangiidae, *Phalangium opilio* (reported as *P.* sp.). Its symbiotic bacterium *Xenorhabdus nematophilus* (Poinar & Thomas) killed the above mentioned arthropod host. This nematode has a wide host range of insects and arachnids (Poinar 1979; Poinar & Thomas 1985; Poinar *et al.* 1985). A thorough description and review of this nematode and its relationship with *X. nematophilus* are provided by Poinar (1979).

Family Heterorhabditidae

Heterorhabditis Poinar is the only genus in the family. It is known by three described species (Poinar & Welch 1981; Poinar 1990), one of which is known to infect harvestmen. Keys to the infective juveniles of the three species is found in Poinar (1990). Adults are identified by electrophoretic analysis of enzymes (Akhurst 1987), DNA fingerprinting and morphology (Poinar *et al.* 1987). The mode of entry into the host and general life cycle follow that listed under *Steinernema*, except that *Heterorhabditis* have a heterogenic life cycle. Maturing females can either be hermaphroditic or amphimictic. The first hermaphroditic generation is usually followed by one or more amphimictic generations in a single cadaver. Juveniles of *Heterorhabditis* can enter host via natural openings, or in smaller, more fragile host by breaking the cuticle with a dorsal (and sometimes ventral) hook.

Heterorhabditis bacteriophora Poinar 1975, is a well-known insect parasite. Considerable literature on this species is listed under a synonym *Heterorhabditis heliothidis* (Khan *et al.* 1976); which was originally described in combination with the new genus *Chromonema* (Khan *et al.* 1976). Poinar & Thomas (1985) demonstrated this nematode could infect and successfully reproduce in the Phalangiidae *Phalangium opilio* (reported as *P.* sp.). Its symbiotic bacterium *Xenorhabdus luminescens* killed the above mentioned host. This nematode has a wide host range of insects and arachnids (Poinar 1979; Poinar & Thomas 1985; Poinar *et al.* 1985). A thorough review of this nematode is provided by Poinar (1979).

Class Adenophorea
Subclass Enoplia
Order Mermithida
Superfamily Mermithoidea
Family Mermithidae

All known mermithid records from harvestmen are based on juvenile nematodes. Consequently, none can be accurately assigned to a

genus (see below under *Agamomermis*). Researchers fortunate enough to obtain adult material should consult the key provided by Poinar (1977).

Matthiesen (1974) reported the discovery of a Gonyleptidae (*Gonyleptes fragilis* Mello-Leitão) which was infested by a internal parasite. Preliminary observations through the harvestman's body (the parasite was apparently not dissected from the host) suggested the parasite to be either a Nematomorpha or mermithid. Because there are no other recorded cases of the former attacking Opiliones, I assume the parasite was a juvenile mermithid.

Unknown species were reported by Poinar (1985) from a Sclerosomatidae [*Togwoteeus* (reported as *Homolophus*) *biceps* (Thorell) from western Canada], a Cosmetidae [*Paecilaemana quadripuncta* Goodnight & Goodnight from Costa Rica] and a Protolophidae [*Protolophus* sp. from the southwestern USA]. Pfeifer (1956) also reported an unknown species from a Phalangiidae, *Phalangium opilio*, from Berlin, Germany.

Tsurusaki (1986) found unidentified mermithids in two species of Sclerosomatidae (*Leiobunum globosum*, *Leiobunum manubriatum*) in Japan.

Mitov reported (pers. commun.) that he had discovered larval mermithids in preserved material of the following harvestmen from Vitosha Mountain and West Rodopy, Bulgaria: Nemastomatidae (*Paranemastoma radewi*), Phalangiidae (*Lacinius ephippiatus*, *L. horridus*, *L. dentiger*, *Lophopilio palpinalis*, *Mitopus morio*, *Phalangium opilio*, *Zacheus crista*).

Agamomermis Stiles is a collective group erected to receive species which were described from larvae (which lack meaningful taxonomic characters) [see Poinar & Welch (1981)]. When diagnosing *Agamomermis*, Stiles (1903) stated the group was artificial and therefore should have no type species. All of the mermithids thus far recorded from harvestmen are considered *incertae sedis* and therefore those species that were originally described from harvestmen should be transferred to *Agamomermis*. This action was indicated but not formally performed by Poinar (1985).

Agamomermis phalangii (Haldeman 1851), new combination, was originally described in combination with *Filaria* Mueller from a Phalangiidae, *Phalangium opilio* (reported as *P. cornutum*). *Agamomermis truncatula* Rudolphi (1819), new combination, was originally described in combination with *Filaria*. Steiner (1922) transferred the species to *Mermis*. The original specimens were from the abdomens of Phalangiidae, *Phalangium opilio* and *Opilio* (reported as *Phalangii cornuti* and *Opilionis*). Diesing (1851) listed the species as "*Gordius truncatulus* Diesing," but it is unclear if he had additional material.

Agamermis incerta was reported by Stipperger (1928) from *Mitopus morio* collected in Tirol, Austria. Stipperger (1928, p. 60) stated that he had sent the specimen to Dr. G. Steiner for identification and that he had received an identification as "*Agamermis incerta* n. sp." Pfeifer (1956) and Poinar (1985) referred to this species as *Agamermis incerta* (Steiner), indicating that it had been described in some other genus. I have been unable to locate the description of this species (in combination with *Agamermis* Cobb, Steiner & Christie; *Hexamermis* Steiner, or *Mermis* Dujardin) in Zoological Record (1918–1940) and presume it is a *nomen nudum*. Apparently, Poinar (1985) also was unable to locate Steiner's description of *incerta* (in combination with *Agamermis* or otherwise) from a spider, as this species of mermithid does not occur in his table except associated with Stipperger's 1928 paper.

Hexamermis sp., *incertae sedis*, juveniles were reported (Unzicker & Rotramel 1970) from an immature Phalangiidae harvestman (*Opilio* sp.–only species in region is *O. parietinus*) from Illinois, USA. Because of the uncertainty of the identification, this species is best retained as *Agamomermis* sp.

Mermis sp. was reported by Kästner (1928). He stated Julius Rühm of Nernberg saw a "Mermis" emerge from a "Phalangiidaen." This record was later cited as Phalangiidae, *Opilio* sp., by Poinar (1985). The only paper by Rühm cited by Kästner was published in 1926 and contained no mention of a *Mermis*. Apparently, there has been some miscommunication regarding this record. Probably, Rühm verbally communicated this observation to Kästner and used "Mermis" as a general term for a mermithid nematode. Furthermore, because the record is of a postparasitic juvenile, the record is correctly attributed to *Agamomermis* sp.

Phylum Nematomorpha

Hairworms are free-living as adults and parasitic as juveniles in insects, spiders and crustaceans. Some early records of mermithid nem-

atodes were incorrectly assigned to two genera (*Filaria* and *Gordius* Linné) belonging to this phylum. Those species are listed herein as *Agamomermis* spp. (see this group under the Nematoda).

Phylum Arthropoda
Class Insecta
Order Diptera
Suborder Cyclorrhapha

The Cyclorrhapha is comprised of many families of flies, each having a different life cycle – most are not parasitoides. Without knowing the identification of the fly, little can be written other than a notice of the single reported occurrence.

Soares (1945) reported the discovery of a fly pupa inside an adult of a Gonyleptidae (*Discocyrtus invalidus* Piza). The gonyleptid was collected at Porto Cabral, Estado de São Paulo, Brazil.

Suborder Nematocera
Family Ceratopogonidae

Tsurusaki (pers. commun.) reported finding adult flies of this family, subfamily Forcipomyiinae, settled on the leg femora of *Nelima nigricoxa* and *Gagrellula ferruginea* in Japan. When he disturbed the flies they would hover around the host. He suspected they were sucking blood from the harvestmen.

Order Hymenoptera
Family Chalcidae

Laniatores (Triaenonychidae and/or Synthetonychidae) from New Zealand are reported by Forster (1954) to be infested by chalcid wasps. No specific identifications were provided.

Family Pompilidae

Anoplius Dufour is a large, diverse group of wasps which prey almost exclusively upon spiders (Evans & Yoshimoto 1962). The female wasps sting and paralyze spiders which are individually entombed with a wasp egg. The wasp young will then devour the spider as it grows. Some of the species permanently paralyze their prey while others only paralyze them temporarily. Some adult wasps feed upon spiders while others feed upon nectar of flowers. Only a single species has been recorded to prey upon a harvestman.

Anoplius (*Pompilinus*) *marginatus* (Say 1824) is found over most of temperate North America east of the Rocky Mountains. It is often common and unlike other pompilids is not very selective as to the prey it takes. Prey items include at least 22 species of spiders from seven different families (Evans & Yoshimoto 1962). Evans (1948) recorded a female wasp taking a Phalangiidae (*Odiellus pictus*) in East Hartford, Connecticut, USA. Because the harvestman was taken away from the wasp before it dug a nest it is uncertain if it would use the *O. pictus* to provision the nest. Evans (pers. commun.) recalled that the wasp was captured while it was dragging the opilion across the ground but he could not determine whether the opilion was used in provisioning the wasp nest. Pompilids often take prey and then abandon it, sometimes after feeding on it.

Class Arachnida
Order Acarina
Suborder Prostigmata

Mites known to be parasitic on harvestmen belong to the families Thrombidiidae and Erythraeidae. Only the larval forms are parasitic (protelean parasites) while the nymphs and adults are predaceous on small insects. Because the larval and post-larval stages of these two families are heteromorphic, systematists have long used different scientific names for each (Southcott 1961). Only after the larval and post-larval stages are associated by rearings can any meaningful classifications be constructed.

Laniatores (Triaenonychidae and/or Synthetonychidae) from New Zealand are reported by Forster (1954) to be often heavily infested by mites. Hunt (1979) found a species of parasitic mite on Triaenonychidae harvestman, *Equitius doriae* Simon, from southeastern Australia. Burton & Burton (1984, pp. 218 and 226) published a color photograph of a harvestman with numerous parasitic red mites. The harvestman is clearly *Mitopus morio*. The mites are probably members of the genus *Leptus*, although this can not be stated for certain. Elliott & Reddell (1987) reported that many of the *Leiobunum townsendi* occurring in caves in central Texas carried red chiggers on their legs. The mites are probably not chiggers but more likely the larvae of *Leptus*. Eaton (1985) stated in a report on some harvestmen from a cave in southeastern, New Mexico that the "The [harvestmen] spiders all had one or more small, shiny, bright red, oval bumps on their legs which appeared to be some kind of parasite." These parasites are likewise probably *Leptus* sp. and the hosts are almost certainly *L. townsendi*.

Other unidentified mites from my collection include: Cosmetidae (*Vonones sayi*) from Sam Houston National Forest, Lake Stubblefield, Walker County, and Lake Kirby, Taylor County, Texas, USA (mites found on dorsa of abdomens); Phalangiidae [*Zacheus hebraicus* (Simon)] from Beith Shemesh, Israel (mite from tibia I); Sclerosomatidae: Leiobuninae (*Leiobunum townsendi* Weed) from near Cloudcroft, New Mexico, USA; [*Leiobunum ventricosum* (Wood)], West Virginia University Forest, Chestnut Ridge, Monongalia County, West Virginia, USA.; (*Nelima paessleri* Roewer) from Moose Creek Research Station, Idaho, USA; Sclerosomatidae: Gagrellinae (*Gagrellopsis nodulifera* Sato & Suzuki) from Mt. Daisen, Tottori Pref., Japan (mite found on dorsum of abdomen); (*Trachyrhinus rectipalpus* Cokendolpher) from 2 km W. of Cuevitas, Starr County and Buffalo Gap, Taylor County, Texas, USA; (*Prionostemma panama* Goodnight & Goodnight) from Orillas de Rio Mata Ahogado el Vallo de Antón, Prov. Coclé, Panama (mite was found on the abdomen); Sclerosomatidae: Metopilio Group (*Globipes* sp.) from near Cloudcroft, New Mexico, USA.

Family Thrombidiidae

Known as the velvet mites, adults of this family are among the largest and most conspicuous families of mites.

Allothrombium Berlese is a small genus with seven described species. Its members are parasitic on harvestmen, spiders, several orders of insects and isopods (Welbourn 1983). Mégnin (1876) described the larva of a mite reared from opilions. He identified the mite as either *Trombidium fuliginosum* Herman or *Trombidium gymnopterorum* Berlese. Based on the structure of the tarsal claws, Southcott (1961) identified Mégnin's specimen (which was illustrated) as an *Allothrombium* sp.

Allothrombium chanaanense Feider (1977) was described from an "Opilionida" from Jerusalem, Israel. This species of mite is only known from the larval forms. Host records also include insects: an Acrididae [*Prionsosthenus galericulatus* (Stål)] and an unidentified Aphidae from Israel (Feider 1977).

Allothrombium neapolitum Oudemans (1910a) was described from a Phalangidae (*Phalangium* sp.) from Portici, Campania, southern Italy. Oudemans (1913) redescribed and illustrated this species. Specimens identified from my collection were found attached to the edges of the abdominal spiracles of a Phalangiidae, *Zacheus crista* Brullé. The collections were from Lindos, Rhodos.

Trombidium Fabricius is a relatively large genus of conspicuous mites with about 20 species. Member species have been observed and recorded since the first record in about 300 B.C. by Apollodorus. About half of the described species are known only by adults. Juveniles are known to feed on numerous orders of insects as well as spiders, a pseudoscorpion and harvestmen (Welbourn 1983).

Yokogawa (1940) described and illustrated a Sclerosomatidae (*Nelima* sp.) parasitized by a mite from Japan. The mite was identified as a "*Trombidinium*" [*sic*]. *Trombidium hungarium* Kobulej (1957) is recorded from a Phalangiidae (*Egaenus convexus* Koch) from Mátraszentimre, Hungary. Both the larva and the nymph of this species were described by Kobulej (1957).

Family Erythraeidae

The first record of a harvestman parasite was probably an erythraeid mite. Lister (1678) reported scarlet-colored "bugs" attached and feeding from what is now known to be Phalangiidae *Phalangium opilio* in England. Sankey (1949b) reported mites of this family from numerous species of harvestmen collected in England. Specifically, he recorded hosts as: Sclerosomatidae [*Leiobunum blackwalli*, *L. rotundum*, *Nelima silvatica* (Simon)] and Phalangiidae [*Mitopus morio*, *Oligolophus hansenii* (Kraepelin), *O. tridens*, *Opilio parietinus*, *Paroligolophus agrestis* (Meade), *Phalangium opilio*, *Rilaena triangularis* (=*Platybunus triangularis*)]. Sankey (1949a) stated that he had records of 10 species of harvestmen (presumably those listed above) being used as carriers by the larvae of *Erythraeus phalangioides* (De Geer 1778). This identification is probably incorrect as this species is not otherwise known to feed on harvestmen and there is some question regarding the true identity of larval *E. phalangiodes* (see Southcott 1961). Possibly, Sankey confused the names *phalangii* and *phalangiodes*; both of which were described by De Geer. Martínez Crespo & Morales Soto (1979) reported that mites of the family Erythraeidae were parasitic on Opiliones from Mexico.

There are over 50 species of *Charletonia* Oudemans described as larvae and 22 species described originally as adults. Species are recorded from every continent except Antarctica (Southcott 1991). Larvae of two species are par-

asitic on harvestmen (Kawashima 1961; Southcott 1961, 1965, 1991). The other species are common parasites as juveniles on locusts (Acrididae) and less commonly encountered on jumping plant lice (Psyllidae: Homoptera), true bugs (Lygaeidae and Miridae: Hemiptera), wasps (Braconidae: Hymenoptera), Lepidoptera, dragonflies (Libellulidae: Odonata), flies (Tabanidae, Dolichopodidae and Bombylidae: Diptera), mantis (Mantidae: Mantodea), walking sticks (Phasmatidae: Phasmida), katydids (Tettigoniidae: Orthoptera), beetles (Curculionidae, Melyridae, Tenebrionidae: Coleoptera), mites (Erythraeidae: Acarina) and spiders (Theridiidae, Philodromidae: Araneae). Keys to the species are provided by Southcott (1991).

Charletonia enghoffi Southcott (1991) is known by four larvae recovered from the dorsum and femora of the Phalangiidae, *Bunochelis canariana* (Strand). The species were obtained in February in Teno Barranco de las Cuevas, Tenerife, Canary Islands.

Charletonia southcotti Kawashima (1961) is recorded from a Sclerosomatidae, *Metagagrella tenuipes* (L. Koch) (reported as *Gagrella japonica* Roewer), that was collected at the seashore of Kasumigaoka, Fukuoka City, Fukuoka-Prefecture, Kyushu, Japan. This species of mite is only known from the single collection on 12 July. Thirty-five mites were recovered from 20 opilions. It is known only by the larval stage, which was redescribed by Southcott (1965).

Leptus Latreille is a large genus and its members are widespread. Over 60 *Leptus* spp. have been described from larvae. Many adults have also been described, but only in a few cases have correlations been made between larval and post-larval forms. Only in a single case is a species described from larval and all post-larval stages (Welbourn & Jennings 1991). Many species remain undescribed. Member species are generally parasitic on spiders, scorpions, harvestmen, diplopods, Collembola, and insects. Many of the early reports and even some more recent are suspect as the true identity of the mites identified is uncertain. Southcott (1961, 1991, 1992) reviewed some of the problems regarding the European mites (*phalangii*, *ignotus*, *nemorum*, *coccineus*) which had been referred to various genera. Southcott (1989) provided a key to the parasitic larval forms that were recognizable (most early descriptions are inadequate to recognize the species) in the New World. Welbourn & Jennings (1991) added a new species (from Lepidoptera host) from the USA and provided some additional comments on members of the genus. Southcott (1992) described numerous new species and provided a key to the taxa from North America and Europe. He also resolved the identity of *L. ignotus* and found the type species, *Acarus phalangii*, to be an illegitimate name. Kawashima (1958) and Haitlinger (1990) provided keys to the parasitic larval forms from Japan and northern Africa, respectively.

Leptus spp. have been reported from a variety of hosts and localities. The mode of attachment was described in *Leptus* sp. on two species of Phalangiidae (*Mitopus morio*, *Phalangium opilio*) by Åbro (1988). Åbro (1991) described unsuccessful parasitic attachments of larval *Leptus* spp. to the ocular tubercle of *Phalangium*. Evans *et al.* (1961, fig. 211) illustrated a Phalangiidae (*Mitopus morio*) infested with *Leptus* sp. larvae from the British Isles. Welbourn (1983) reported *Leptus* spp. from unidentified Opiliones collected in Ohio and Arkansas.

Robert G. Holmberg reported (pers. commun.) that he had found 39 vials of harvestmen infested with 78 mites, all of which have been identified as *Leptus* spp. by I. M. Smith (Biosystematic Research Center, Ottawa, Canada). Dr. Holmberg's collections were from: "*Togwoteeus biceps* from Canada and the USA, *Mitopus morio* from England, *Odiellus pictus* from Canada, *Oligolophus tridens* from Canada, *Paroligolophus agrestis* from Wales, *Phalangium opilio* from Canada and England, and *Leiobunum townsendi* from U.S.A."

Mullen (1988) reported "opilionids" commonly serve as the host to *Leptus* mites. Savory (1938) recorded *Belaustium* [sic] (*Ritteria*) *nemorum* (Koch) from harvestmen in England. This observation was later cited on several occasions in general works about arachnids by Savory and Cloudsley-Thompson. The original observations were most likely based on a misidentification and probably were representatives of the genus *Leptus*. Not only is *Leptus* widely known as a harvestman parasite, but members of the Balaustiinae are generally considered not to be parasitic on arthropods (Southcott 1961).

Cox *et al.* (1921) found an immature *Erythaeus* [sic] sp. on a "phalangid" in California, USA. This mite is probably a *Leptus* sp. Mites from almost every genus of the Erythraeidae have been misidentified as *Erythraeus* Latreille (see Southcott 1961).

Leptus phalangii (De Geer 1778) was originally described in combination with *Acarus* Linné. When erecting the genus *Leptus*, Latreille (1796) designated (by monotypy) *Acarus phalangii* as the type species. The type specimens were from a Phalangiidae (*Phalangium* sp.) collected in Sweden. Apparently, none of De Geer's specimens were preserved. There has been considerable confusion over the identity of this species. Furthermore, as noted by Southcott (1992) the specific name is not available under the International Code of Zoological Nomenclature as De Geer did not treat it consistently as a binomen. Only in a few cases can specimens that have been previously referred to in the literature as *Leptus phalangii* be assigned currently recognized names.

Leptus ignotus (Oudemans 1903a) was originally described in combination with *Erythraeus*. The type locality is Borkum, Holland. Southcott (1991) redescribed the species and limited the species diagnosis to specimens which had not been recorded from opilion hosts. Therefore all records of this species from opilion host can be assumed to be misidentified and are referred to in Table 1 as *Leptus* sp. Evans *et al.* (1961) recorded a mite (identified as *L. ignotus*) parasitic on *Opilio parietinus* in the British Isles. Other records are also from the Phalangiidae: *Mitopus morio* from Tirol, Austria (Stipperger 1928) and Bulgaria (Beron 1975); *Opilio ruzickai* from Bulgaria (Beron 1975); and *Phalangium opilio, R. triangularis, Lophopilio* (reported as *Odiellus*) *palpinalis* from Poland (Haitlinger 1987). Southcott (1992) suggested that some of the specimens identified by Beron and Haitlinger were *Leptus holmiae* Southcott.

Mites reported as *Leptus phalangii* have been reported by Pfeifer (1956) and Evans (1910) on Phalangiidae (*Phalangium opilio*) in Berlin, Germany, and Midlothian, Scotland, respectively. Spoek (1964) also recorded this mite to be parasitic on harvestmen from the Netherlands. None of these mites can be accurately identified at present and are best referred in Table 1 as *Leptus* sp. Meade (1855) reported "harvest-men" from England were frequently infested by a bright red parasitic mite, which he identified as *Trombidium phalangii* (=*Leptus phalangii*). He further specified that the mite occurred on *Leiobunum rotundum*.

Sellnick (1940) recorded both *Achorolophus ignotus* and *Leptus* (reported elsewhere in the paper as *Erythraeus*) *phalangioides* (De Geer) from Phalangiidae (*M. morio*) on Iceland. He not only recorded both mites from a single species of harvestmen, but in two cases he recorded what he felt were these species from individual harvestmen. Although these cannot be identified with certainty at this time, they are probably *L. holmiae*. Until specimens can be studied I am referring to them in Table 1 as *Leptus* sp.

Numerous mites from opilions in my collection represent new records and include: Sclerosomatidae: *Eumesosoma roeweri* (Goodnight & Goodnight) from Alma, Nebraska, USA.; *Krusa* sp. from 10 mi. W. Aquismon, San Luis Potosí, México; *Leiobunum aldrichi* Weed from Tishomingo State Park, Tishomingo County, Mississippi, USA; *Leiobunum flavum* Banks from Beaver's Bend State Park, McCurtain County, Oklahoma; Merrymount Campground, 18 miles SW Nashville, Davidson, Tennessee, USA; *Leiobunum montanum montanum* Suzuki from Mt. Ischizuchi, 1490-1745 m., Ehime Prefecture, Japan; *Leiobunum* sp. from 2 km. N. Tasquillo, Rio Tula, Hidalgo, México; *Leiobunum* sp. nr. *depressum* Davis from 7.5 miles S. George West, Live Oak County, Texas, USA.; *Leiobunum townsendi* from East Turkey Creek, Chiracahua Mountains, Cochise County, Arizona; outside Hidden Cave (reared to deutonymph) and Hermit Cave, Eddy County, New Mexico, USA.; *Leiobunum vittatum* (Say) from Homesville, Nebraska, USA.; *Trachyrhinus marmoratus* Banks from Pecos River, east of Pecos, Pecos County, and Indio Mountains, 25 km S Van Horn, Hudspeth County, Texas, USA. Phalangiidae: *Odiellus pictus* from Garland, Penobscot County, Maine, USA.; *Phalangium opilio* from Bowdoinham, near Cathance River, Sagahahoc County, Maine, USA.

Additional mites from my collection have been identified by W. Calvin Welbourn as *Leptus* spp. 1–11. They are as follows: *Leptus* sp. 1 is known from a Sclerosomatidae (*Leiobunum townsendi*) and a Protolophidae (*Protolophus singularis* Banks) from Fort Bayard, Grant County, New Mexico, USA. *Leptus* sp. 2 is known from several species of Sclerosomatidae: *Eumesosoma roeweri* from 14 miles E. Burnet, Burnet County, Texas; 7.5 miles ESE Bandera, Bandera County, Texas; Texas Tech University Center, Junction, Kimble County, Texas, USA; *Leiobunum flavum* Banks from Graham Creek, 5 miles SSE Zavalla, Angelina County, Texas, USA; *Leiobunum townsendi* from Montague County, Texas, USA. *Leptus* sp. 3 is known from two species of Scle-

rosomatidae (*Leiobunum aldrichi*, *L. nigripes* Weed) from the W. Bank of J. Percy Priest Lake, Elm Hills Park, Davidson County, Tennessee, USA. *Leptus* sp. 4 is known from a Phalangiidae (*Egaenus convexus*) from Bürgenland, Ruster Hügelland, Austria. *Leptus* sp. 5 is known from a Sclerosomatidae (*Trachyrhinus marmoratus* Banks) from 39.6 miles SW Marfa, Presidio County, Texas, USA. *Leptus* sp. 6 is known from a Sclerosomatidae [*Marthana nigerrima* (Müller)] from Tuba Mountains, S. Palawan Cabar, Palawan, Philippines. *Leptus* sp. 7 is known from a Sclerosomatidae (*Eumesosoma*? sp.) from Joya de Juan Mesa (outside), near La Laguna, Tamaulipas, Mexico. *Leptus* sp. 8 is known from a Sclerosomatidae (*Leiobunum* sp.) from km 120 marker on Highway 70, San Luís Potosí, México. *Leptus* sp. 9 is known from a Sclerosomatidae (*Leiobunum* sp.) from roadcut at Gomez Farias, Tamaulipas, México. *Leptus* sp. 10 is known from a Sclerosomatidae (*Lacinius ephippiatus*) from Wr. Wald, Latisberg (Cobenze) E-Mg *ca.* 380–400 m, Wien XIX, Austria. *Leptus* sp. 11 is known from a Phalangiidae (*Mitopus morio)* from Wr. Wald, Rekawiokel, near Bldf., N. G., Austria.

Leptus bicristatus Fain & Elsen (1987) was described from a larva on an "Opilion" from Chowo Rocks, Plateau de Nyika, Malawi (6–8 December 1981). The host has now been identified as a Phalangiidae, *Cristina lettowi* (Roewer) (Kauri, pers. commun.).

Leptus gagrellae (Oudemans 1910b) was originally described in combination with *Achorolophus* Berlese. It was described from a Sclerosomatidae (*Gagrella* sp.) from Tjibodas, West Java Prov., Indonesia. This species was redescribed and illustrated by Oudemans (1913).

Leptus hidakai Kawashima (1958) was described from larvae collected on a Clubionidae spider (*Chiracanthium* sp.) and a Phalangiidae (*Opilio pentaspinulatus* Suzuki). All specimens were obtained on 24 June at Tachibana-yama, Kasuya-gun, Fukuoka Prefecture, Japan. A harvestmen is illustrated in the original description with eight mites attached to its legs and abdomen.

Leptus holmiae Southcott (1992) is a wide-ranging species in the Holarctic region. It is recorded (Southcott 1992) from a free living-example collected in the Burzyanskij region, Bashkir ASSR; and as ectoparasites on Phalangiidae: *Mitopus morio* from Denmark, Iceland, Poland, Sweden; *Opilio* sp. from Sweden; *Opilio canestrinii* (Thorell) from Denmark; *Phalangium opilio* from England; *Rileana* (reported as *Platybunus*) *triangularis* from England. Southcott (1992) stated that he felt some additional specimens reported in the literature might be this species but that he could not be certain because he had not studied any samples of the series reported. These questionable records are Phalangiidae: *Mitopus morio* and *Opilio ruzickai* from Bulgaria (Beron 1975); and *Phalangium opilio*, *R. triangularis*, *Lophopilio* (reported as *Odiellus*) *palpinalis* from Poland (Haitlinger 1987).

Leptus indianensis Fain *et al.* (1987) was described from larvae collected on several species of Sclerosomatidae: *Leiobunum aldrichi* (reported as *L. longipes*) and *Leiobunum calcar* (Wood) from 2 miles northwest Brazil, Clay County, Indiana, USA.; *Leiobunum* sp., *L. nigripes, L. speciosum* Banks and *L. ventricosum* from 9 miles southwest of Crawfordsville, Montgomery County, Indiana, USA. New records from my collection include *L. nigripes* Weed from 4 miles ESE Morris on Pine Bluff Road, Grundy County, Illinois, USA.; *L. formosum* (Wood) from Potomac River and Chesapeake Bay junction, Wakefield, Virginia, USA.

Leptus jocquei Fain & Elsen (1987) was described from nine larvae taken from "Opilions" collected in Dembo, Plateau Nyika, Malawi (5–20 December 1981). The host has now been identified as a Phalangiidae, *Cristina lettowi* (Kauri, pers. commun.).

Leptus kalaallus Southcott (1992) is thus far known only from the Phalangiidae, *Mitopus morio*, collected in Greenland. The larval mites were found attached to the opilion abdomens.

Leptus lomani (Oudemans 1903b) was described from a Gonyleptidae, *Lycomedicus* (reported *Discocyrtus*) *funestus* (Butler), from Chile. This species was redescribed and illustrated by Oudemans (1913). The original series of 10 mites was reported to have been collected by J. C. C. Loman in 1900. Other sources indicate that Jan C. C. Loman, of Amsterdam, did not collect the specimens himself. The harvestmen were probably collected by Prof. Dr. Ludwig Plate and forwarded to Oudemans by Loman. The only examples of this harvestman reported in the literature from Chile during the same time period was by Loman (Cekalovic K. 1985). Loman (1899) stated that there were several specimens of *L. funestus* from Corral that were in the Plate collection. Therefore, I am herein restricting the type locality of *L. lomani* to Corral (39°53′S, 73°25′W), Valdivia, Chile.

Leptus nearcticus Fain *et al.* (1987) was described from larvae collected off three species of

Sclerosomatidae: *Leiobunum aldrichi* (reported as *L. longipes*), *L. nigripes* and *L. vittatum* from 2 miles northwest Brazil, Clay Co., Indiana (1–18 September 1986). Fain *et al.* (1987) reported other samples from the type locality from *Leiobunum* sp. (females). These have now been identified as *L. aldrichi*.

Leptus oudemansi (Karppinen 1958) was original proposed as a replacement name in the genus *Achorolophus*. This name was provided because *Achorolophus gracilipes* Oudemans 1910a, was preoccupied by *Rhyncholophus gracilipes* Kramer 1897; both were considered by Karppinen (1958) to belong to *Achorolophus*. Both are now considered by Southcott (1992) to belong to *Leptus* and are thus still homonyms. Oudemans' (1910a) original specimens were found on a Cosmetidae (*Cynorta* sp.) from Surinam. This species was redescribed and illustrated by Oudemans (1913).

Leptus puylaerti Fain & Elsen (1987) is known by five larvae found attached to "Opilions" collected at Chowo Rocks, Nyika Plateau, Malawi (6–18 Dec. 1981). The host has now been identified as a Phalangiidae, *Cristina lettowi* (Kauri, pers. commun.).

Leptus polythrix Fain & Elsen (1987) is known by eight larvae found attached to "Opilions" collected at Dembo, Nyika Plateau, Malawi (5–20 December 1981). The host has now been identified as a Phalangiidae, *Cristina lettowi* (Kauri, pers. commun.).

Leptus stieglmayri (Oudemans 1905) was described from Opiliones collected in Santa Cruz, Rio Grande do Sul, Brazil. Oudemans (1913) redescribed this species and recorded a specimen that was collected from a beetle (Cleridae) collected in Brazil.

A probable new genus (near *Leptus*) is under study by W. Calvin Welbourn. Thus far, members are only known from harvestmen from my collection obtained in Chile. The new specimens are known from two species of Neopilionidae (*Thrasychirus modestus* Simon, *Thrasychirus dentichelis* Simon) from Isla Deceit Caleta Toleda, archipiélago Cabo de Hornos, Magallanes, Chile. This is the southern most record for a harvestman parasite. Other host records include species of Gonyleptidae: *Eubalta meridionalis* (Sörensen) from Reserva Forestal Magallanes, 8 km west Punta Arenas, Magallanes, Chile; *Metagyndes pulchella* (Loman); Niebla, near Valdivia, Chile; *Acanthoprocta pustulata* Loman from Cerro Nielol, Temuco, Chile.

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Table 1.—List of pathogens and parasites grouped by opilion host.

Host	Parasite	Source
Family? *incertae sedis*		
harvestmen, England	?*Leptus* sp.	Evans 1910; Savory 1938
harvestmen, Netherlands	*Leptus* sp.	Spoek 1964
Opliones, Brazil	*Leptus stieglmayri*	Oudemans 1905
Opiliones, Mexico	Erythraeidae	Martínez Crespo and Morales Soto 1979
Opiliones, U.S.A	*Leptus* spp.	Welbourn 1983
Opilionidé, Israel	*Allothrombium chanaanense*	Feider 1977
opilionids	*Leptus* sp.	Mullen 1988
phalangid, U.S.A	?*Leptus* sp.	Cox et al. 1921
Phalangium crassum, France	*Sciadiophora phalangii*	Léger 1897
Suborder Laniatores		
Family Triaenonychidae and/or Synthetonychidae		
gen. sp., New Zealand	Acarina, gen. sp.	Forster 1954
	Chalcidae, gen. sp.	Forster 1954
	Nematoda, gen. sp.	Forster 1954
Family Triaenonychidae		
Equitius doriae	Acarina, gen. sp.	Hunt 1979
	Gregarinasina, gen. sp.	Hunt 1979
Family Assamidae		
Oppalnia sp., India	*Arachnocystis arachnoidea*	Devdhar 1962; Devdhar and Gourishankar 1971
	Contospora opalniae	Devdhar 1962; Devdhar and Amoji 1978a
	Echinoocysta phalangii	Amoji and Devdhar 1979
Family Gonyleptidae		
gen. sp. Brazil	*Torrubiella gonylepticida*	Möller 1901
Acanthoprocta pustulata	N. gn. nr. *Leptus* sp.	herein
Discocyrtus invalidus	Cyclorrhapha, gen. sp.	Soares 1945
Eubalta meridionalis	N. gn. nr. *Leptus* sp.	herein
Gonyleptes fragilis	*Agamomermis* sp.	Mattheisen 1974
Lycomedicus funestus	*Leptus lomani*	Oudemans 1903b
Metagyndes pulchella	N. gn. nr. *Leptus* sp.	herein
Zygopachylus albomarginis	Eumycota, gen. sp.	Mora 1987
Family Cosmetidae		
Cynorta sp.	*Leptus oudemansi*	Oudemans 1910a
Paecilaemana quadripuncta	*Agamomermis* sp.	Poinar 1985
Vonones sayi	Acarina, gen. sp.	herein
	Cosmetophilus vonones	Cokendolpher 1991
Suborder Cyphopalpatores		
Superfamily Troguloidea		
Family Troguloidae		
Trogulus tricarinatus	*Doliospora troguli*	Geus 1969
Family Nemastomatidae		
Carinostoma ornatum	Gregarinasina, gen. sp.	herein
Paranemastoma radewi	Gregarinasina, gen. sp.	herein

Table 1.—Continued.

Host	Parasite	Source
	Agamomermis sp.	herein
Pyza bosnica	Gregarinasina, gen. sp.	herein
Superfamily Phalangioidea		
Family Neopilionidae		
Thrasychirus dentichelis	N. gn. nr. *Leptus* sp.	herein
Thrasychirus modestus	N. gn. nr. *Leptus* sp.	herein
Family Protolophidae		
Protolophus sp., U.S.A.	*Agamomermis* sp.	Poinar 1985
Protolophus singularis	*Leptus* sp. #1	herein
Family Sclerosomatidae		
Metopilio group		
Globipes sp.	Acarina, gen. sp.	herein
Subfamily Leiobuninae		
Eumesosoma? sp.	*Leptus* sp. #7	herein
Eumesosoma roeweri	*Leptus* sp.	herein
	Leptus sp. #2	herein
Leiobunum sp., U.S.A.	*Leptus indianensis*	Fain et al. 1987
Leiobunum sp. near *depressum,* U.S.A.	*Leptus* sp.	herein
Leiobunum sp., Hidalgo, Mexico	*Leptus* sp.	herein
Leiobunum sp., San Luis Potosí, Mexico	*Leptus* sp. #8	herein
Leiobunum sp., Tamaulipas, Mexico	*Leptus* sp. #9	herein
Leiobunum aldrichi (=*Leiobunum longipes*)	*Leptus* sp.	herein
	Leptus sp. #3	herein
	Leptus indianensis	Fain et al. 1987
	Leptus nearcticus	Fain et al. 1987
Leiobunum blackwalli (=*L. hassiae*)	*Anthorhynchus sophiae*	Pfeifer 1956
	Entomophaga batkoi	Bałazy 1978
	Erythraeidae, gen. sp.	Sankey 1949b
Leiobunum calcar	*Leptus indianensis*	Fain et al. 1987
Leiobunum globosum	*Agamomermis* sp.	Tsurusaki 1986
	Gregarinasina, gen. sp.	Tsurusaki 1986
Leiobunum flavum	*Leptus* sp.	herein
	Leptus sp. #2	herein
Leiobunum formosum	*Leptus indianensis*	herein
Leiobunum manubriatum	*Agamomermis* sp.	Tsurusaki 1986
	Gregarinasina, gen. sp.	Tsurusaki 1986
Leiobunum montanum montanum	*Leptus* sp.	herein
Leiobunum nigripes	*Leptus* sp. #3	herein
	Leptus indianensis	Fain et al. 1987; herein
	Leptus nearcticus	Fain et al. 1987
Leiobunum politum	Gregarinasina, gen. sp.	herein
Leiobunum rotundum	*Anthorhynchus longispora*	Ormières and Baudoin 1973
	Anthorhynchus sophiae	Pfeifer 1956
	Doliospora repelini	Ormières and Baudoin 1973

Table 1.—Continued.

Host	Parasite	Source
	Entomophaga batkoi	Batazy 1978
	Erythraeidae, gen. sp.	Sankey 1949b
	Leptus sp.	Meade 1855
	Sciadiophora phalangii	Pfeifer 1956
Leiobunum rumelicum	Gregarinasina, gen. sp.	herein
Leiobunum speciosum	*Leptus indianensis*	Fain et al. 1987
Leiobunum townsendi	Acarina, gen. sp.	Elliott and Reddell 1987; herein
	Leptus sp.	herein
	Leptus sp. #1	herein
	Leptus sp. #2	herein
Leiobunum ventricosum	Acarina, gen. sp.	herein
	Leptus indianensis	Fain et al. 1987
Leiobunum vittatum	*Leptus* sp.	herein
	Leptus nearcticus	Fain et al. 1987
	Nomuraea atypicola	Greenstone et al. 1988
Nelima sp., Japan	*Trombidium* sp.	Yokogawa 1940
Nelima nigricoxa	Forcipomyiinae, gen. sp.	herein
Nelima paessleri	Acarina, gen. sp.	herein
Nelima silvatica	Erythraeidae, gen. sp.	Sankey 1949b
Togwoteeus biceps	*Agamomermis* sp.	Poinar 1985
	Leptus sp.	herein
Subfamily Gagrellinae		
Gagrella sp., Indonesia	*Leptus gagrellae*	Oudemans 1910b
Gagrellopsis nodulifera	Acarina, gen. sp.	herein
Gagrellula ferruginea	Forcipomyiinae, gen. sp.	herein
Gagrellula saddlana	*Sciadiophora gagrellula*	Devdhar 1962; Devdhar and Amoji 1978b
Krusa sp., Mexico	*Leptus* sp.	herein
Marthana nigerrima	*Leptus* sp. #6	herein
Metagagrella tenuipes	*Charletonia southcotti*	Kawashima 1961
Prionostemma panama	Acarina, gen. sp.	herein
Trachyrhinus marmoratus	*Leptus* sp.	herein
	Leptus sp. #5	herein
Trachyrhinus rectipalpus	Acarina, gen. sp.	herein
Family Phalangiidae		
gen. sp., England	*Hymenostilbe verrucosa*	Leatherdale 1970
	Pandora phalangicida	Leatherdale 1970
gen. sp., Germany	*Sciadiophora caudata*	Rössler 1882
	Sciadiophora fissidens	Rössler 1882
gen. sp., Sweden	*Pandora phalangicida*	Lagerheim 1898
Subfamily Phalangiinae		
Bunochelis canariana	*Charletonia enghoffi*	Southcott 1991
Cristina lettowi	*Leptus bicristatus*	Fain & Elsen 1987
	Leptus jocquei	Fain & Elsen 1987
	Leptus polythrix	Fain & Elsen 1987
	Leptus puylaerti	Fain and Elsen 1987
Phalangium sp., Italy	*Allothrombium neapolitum*	Oudemans 1910a

Table 1.—Continued.

Host	Parasite	Source
Phalangium sp., Sweden	*Leptus* sp.	De Geer 1778
Phalangium sp., Europe	*Sciadiophora phalangii*	Geus 1969
Phalangium opilio (=*Phalangium cornutum*)	*Agamomermis* sp.	Pfeifer 1956; herein
	Agamomermis phalangii	Haldeman 1851
	Agamomermis truncatula	Rudolphi 1819
	Anthorhynchus sophiae	Schneider 1887; Ormières and Baudoin 1973
	Brachylecithum sp.	Gabrion and Ormières 1973
	Digenea, gen. sp.	Creplin 1846
	Doliospora repelini	Léger 1897; Ormières and Baudoin 1973
	Erythraeidae, gen. sp.	Sankey 1949b
	Gregarinasina, gen. sp.	herein
	Heterorhabditis heliothidis	Poinar and Thomas 1985
	Leptus sp.	Evans 1910; Pfeifer 1956; Åbro 1988, 1991; herein
	Leptus holmiae	Southcott 1992
	Leptus holmiae?	Haitlinger 1987
	Pandora phalangicida	Ellis 1956; Leatherdale 1958, 1970
	Pseudhymenolepis redonica	Gabrion 1977
	Rhabditida, gen. sp.	Pfeifer 1956
	Sciadiophora caudata	Rössler 1882; Ormières and Baudoin 1973
	Sciadiophora fissidens	Rössler 1882
	Sciadiophora geronowitschi	Johansen 1894
	Sciadiophora phalangii	Léger 1897; Geus 1969
	Steinernema carpocapsae	Poinar and Thomas 1985
	Xenorhabdus luminescens	Poinar and Thomas 1985
	Xenorhabdus nematophilus	Poinar and Thomas 1985
Rilaena triangularis (=*Platybunus triangularis*)	*Anthorhynchus sophiae*	Pfeifer 1956
	Erythraeidae, gen. sp.	Sankey 1949b
	Leptus holmiae	Southcott 1992
	Leptus holmiae?	Haitlinger 1987
	Nematoda, gen. sp.	Sankey 1949a
	Sciadiophora phalangii	Pfeifer 1956
Zacheus anatolicus	Gregarinasina, gen. sp.	herein
Zacheus crista	*Agamomermis* sp.	herein
	Allothrombium neapolitum	herein
	Gregarinasina, gen. sp.	herein
Zacheus hebraicus	Acarina, gen. sp.	herein
Subfamily Oligolophinae		
Lacinius ephippiatus	*Agamomermis* sp.	herein

Table 1.—Continued.

Host	Parasite	Source
	Anthorhynchus sophiae	Pfeifer 1956
	Gregarinasina, gen. sp.	herein
	Leptus sp. #10	herein
Lacinius dentiger	*Agamomermis* sp.	herein
	Gregarinasina, gen. sp.	herein
	Sciadiophora phalangii	Šilhavý 1961
Lacinius horridus	*Agamomermis* sp.	herein
	Gregarinasina, gen. sp.	herein
	Rhabditida, gen. sp.	Pfeifer 1956
Mitopus morio (=*Opilio grossipes*)	Acarina, gen. sp.	Burton and Burton 1984
	Agamomermis sp.	Stipperger 1928; herein
	Anthorhynchus longispora	Ormières and Baudoin 1973
	Anthorhynchus sophiae	Pfeifer 1956
	Doliospora repelini	Ormières and Baudoin 1973
	Erythraeidae, gen. sp.	Sankey 1949b
	Gregarinasina, gen. sp.	herein
	Leptus sp.	Stipperger 1928; Evans et al. 1961; Åbro 1988; herein
	Leptus sp. #11	herein
	Leptus holmiae	Southcott 1992
	Leptus holmiae?	Sellnick 1940; Beron 1975
	Leptus kalaallus	Southcott 1992
	Sciadiophora caudata	Rössler 1882; Ormières and Baudoin 1973
	Sciadiophora phalangii	Stipperger 1928; Pfeifer 1956; Ormières and Baudoin 1973
Mitopus sp., France	*Sciadiophora claviformis*	Ormières and Baudoin 1973
Odiellus lendli	Gregarinasina, gen. sp.	herein
Odiellus pictus	*Anoplius marginatus*	Evans 1948
	Gregarinasina, gen. sp.	herein
	Leptus sp.	herein
Odiellus spinosus (=*Odius spinosus*)	*Sciadiophora caudata*	Rössler 1882; Ormières and Baudoin 1973
Oligolophus hansenii	Erythraeidae, gen. sp.	Sankey 1949b
Oligolophus tridens	*Anthorhynchus sophiae*	Ormières and Baudoin 1973
	Doliospora repelini	Ormières and Baudoin 1973
	Entomophaga batkoi	Bałazy 1978; Keller 1987
	Erythraeidae, gen. sp.	Sankey 1949b
	Leptus sp.	herein
Paroligolophus agrestis	Erythraeidae, gen. sp.	Sankey 1949b
	Leptus sp.	herein
Subfamily Opilioninae		
Egaenus convexus	*Leptus* sp. #4	herein
	Trombidium hungarium	Kobulej 1957
Opilio sp., Europe	*Agamomermis* sp.	Kastner 1928
	Agamomermis truncatula	Rudolphi 1819

Table 1.—Continued.

Host	Parasite	Source
	Leptus holmiae	Southcott 1992
Opilio canestrinii	*Leptus holmiae*	Southcott 1992
Opilio dinaricus	Gregarinasina, gen. sp.	herein
Opilio parietinus	*Agamomermis* sp.	Unzicker and Rotramel 1970
	Anthorhynchus longispora	Ormières and Baudoin 1973
	Doliospora repelini	Ormières and Baudoin 1973
	Erythraeidae, gen. sp.	Sankey 1949b
	Leptus sp.	Evans et al. 1961
	Microsporidium weiseri	Šilhavý 1960
	Sciadiophora phalangii	Pfeifer 1956
Opilio pentaspinulatus	*Leptus hidakai*	Kawashima 1958
Opilio ruzickai	Gregarinasina, gen. sp.	herein
	Leptus holmiae?	Beron 1975
Opilio saxatilis	Gregarinasina, gen. sp.	herein
Subfamily Platybuninae		
Lophopilio palpinalis (=*Odiellus palpinalis*)	*Agamomermis* sp.	herein
	Gregarinasina, gen. sp.	herein
	Leptus sp.	Haitlinger 1987
	Leptus holmiae?	Haitlinger 1987
	Sciadiophora fissidens	Rössler 1882
Megabunus diadema	*Actinocephalus megabuni*	Ormières and Baudoin 1973
	Doliospora repelini	Ormières and Baudoin 1973
Platybunus bucephalus	Anthorhynchus *longispora*	Ormières and Baudoin 1973
	Doliospora repelini	Ormières and Baudoin 1973
	Sciadiophora phalangii	Ormières and Baudoin 1973
Platybunus pinetorum	*Sciadiophora phalangii*	Pfeifer 1956

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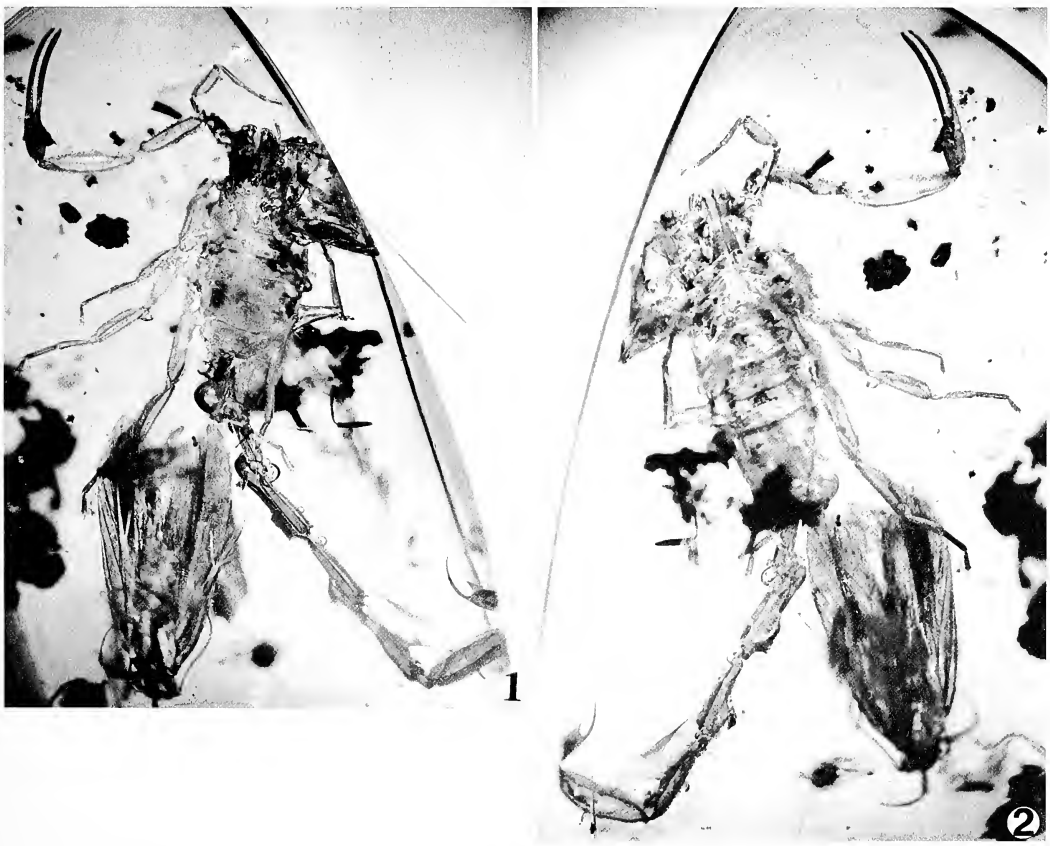
RESEARCH NOTES

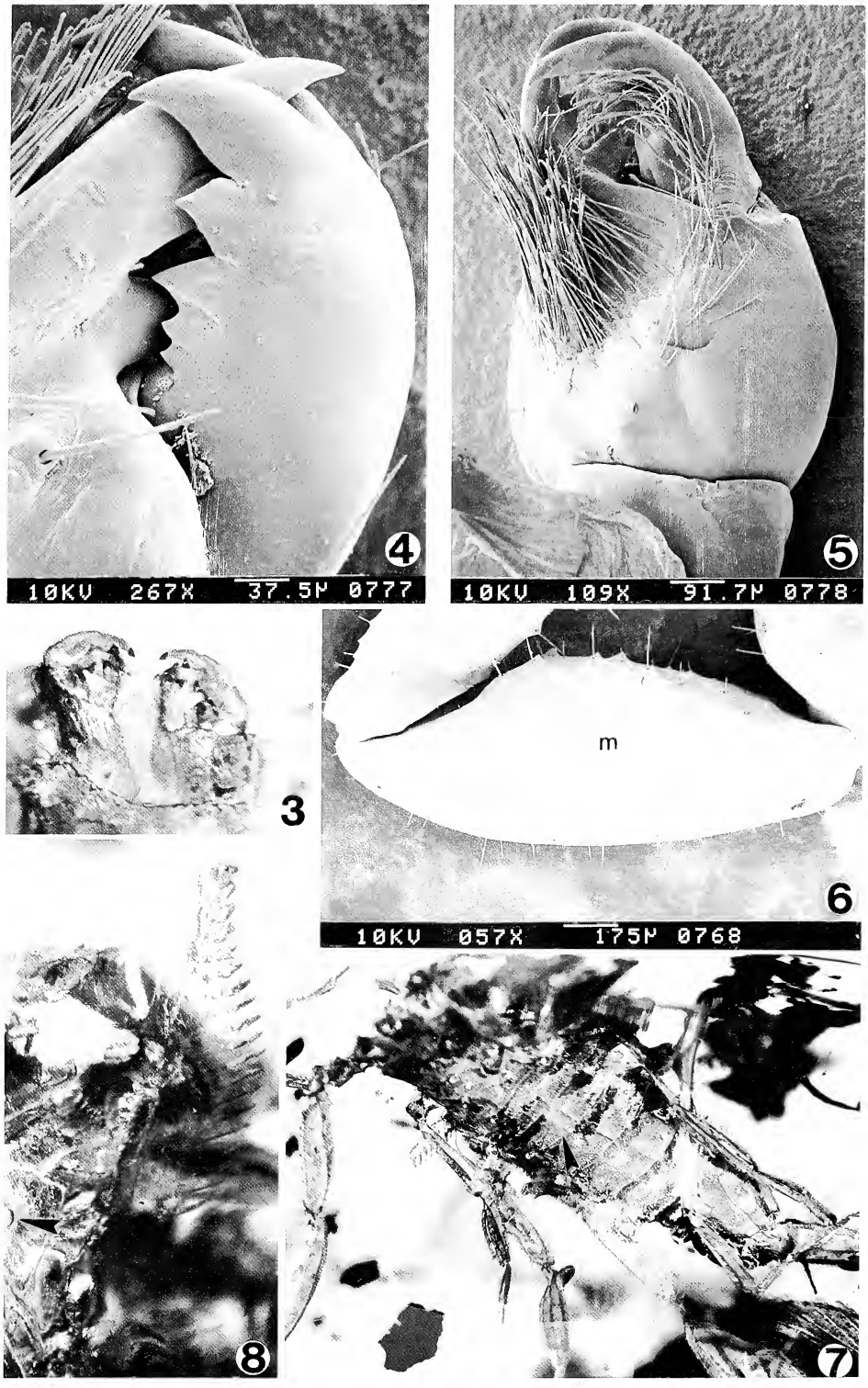
FIRST SCORPION (BUTHIDAE: *CENTRUROIDES*) FROM MEXICAN AMBER (LOWER MIOCENE TO UPPER OLIGOCENE)

A juvenile scorpion, moderately well-preserved in Chiapas (México) amber collected in February 1992 came to our attention (Figs. 1, 2). The relatively elongated metasomal segments suggest that the specimen is a male, probably a *Centruroides* (Marx 1890) (Buthidae). The specimen, which lacks most of its right pedipalp, is the first scorpion reported from Chiapas amber. *Centruroides beynai* Schawaller 1979 (see also Schlee 1980), *Microtityus ambarensis* (Schawaller 1982) (see also Santiago-Blay, Schawaller & Poinar 1990; Schawaller 1984), and *Tityus geratus* (Santiago-Blay & Poinar 1988) are known from Dominican amber.

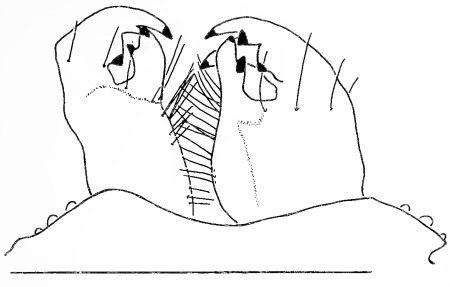
The piece containing the fossil is believed to have originated from mines near the village of Simojovel (State of Chiapas). The amber in the Simojovel mines is located in a sequence of primarily marine calcareous sandstones and silt with beds of lignite. The amber-bearing strata extend from the Balumtun Sandstone of the lower Miocene to the La Quinta formation of the upper Oligocene. These deposits have been assigned to the planktonic foraminiferal zones N3 and N4



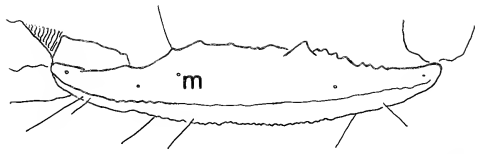
Figures 1, 2.—*Centruroides*? sp. from Chiapas (México) amber: 1. dorsal, overall; 2. ventral, overall.



Figures 3–8.—*Centruroides*? from Chiapas (México) amber: 3, chelicera (see also Fig. 9), dorsal; 4, chelicera of *C. gracilis* nymph, right, dorsal; 5, chelicera of *C. gracilis* nymph, left, ventral; 6, left pedipalp patella of *C. nitidus* nymph, ventral. Note microsetae (m); 7, *Centruroides*? sp. from Chiapas (México) amber. Mesosomal



9



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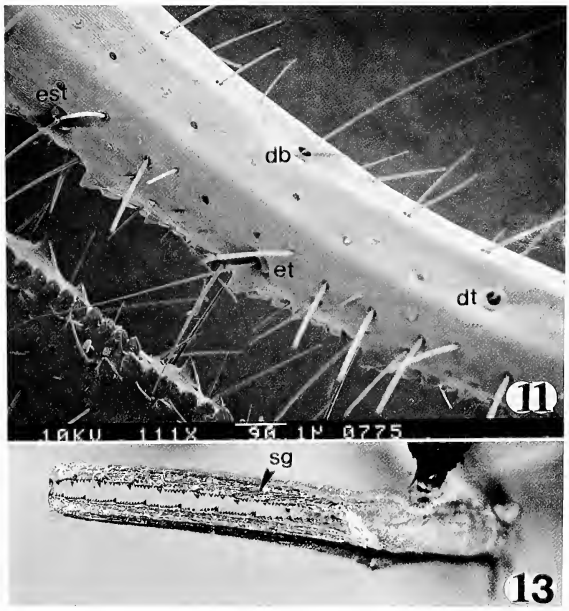
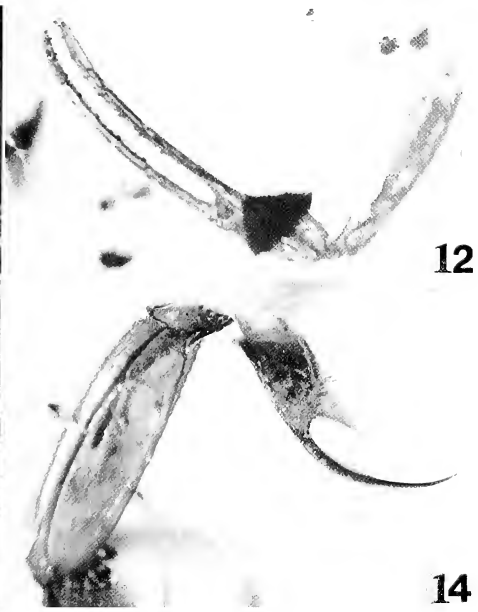
Figures 9, 10.—*Centruroides*? sp. from Chiapas (México) amber. 9, chelicera; 10, pedipalp patella venter, dots indicate possible microsetal (m) insertions. Scale lines = 1 mm.

in the Cenozoic Planktonic Foraminiferal Zonal Sequence and radiometrically dated from 22.5–26 million years (Berggren & Van Couvering 1974). It should be noted that the amber deposits are secondary; thus, the above dates provide a minimum age.

Owing to the scarcity of published data on the systematics and ontogeny of extant, juvenile *Centruroides* and to the problems of interpreting several important structures, which are confounded by imperfect preservation of this specimen, the authors prefer to document the find





Figures 11–14.—11, distal end of fixed pedipalp finger of *Rhopalurus princeps* (Karsch 1879) nymph. (The distal most fixed finger trichobothria are dt, db, et, and est). Note rows of denticles on movable finger and suggestion of supernumerary granules, sg); 12, *Centruroides*? sp. from Chiapas (México) amber, left pedipalp chela, dorsal; 13, *Centruroides*? sp. from Chiapas (México) amber, retrolateral; 14, *Centruroides*? sp. from Chiapas (México) amber, fifth metasomal segment and telson.

←

keel-like structures (arrow head), dorsal; 8, *Centruroides*? sp. from Chiapas (México) amber. Sternopectinal area. Note apodeme-like structure (arrow head) of problematic interpretation—an artifact?

rather than describing this scorpion as a new taxon, pending acquisition of additional specimens from Chiapas.

Centruroides? sp.
(Figs. 1–3, 7–10, 12–14)

Possibly a fourth instar juvenile male, 17.1 mm long, pale-yellowish brown, with pedipalp chela and V metasomal segment dark brown, suggestion of two longitudinal bands on mesosomal tergites 2–3; possibly 8 primary rows of denticles on pedipalp fingers, supernumerary granules obsolete (Figs. 12, 13); pectines with 18–19 teeth (Fig. 8); metasomal segments I–V with 10, 8, 8, 8, and 5 complete, crenulated keels; very well-developed subaculear tooth (Fig. 14). Measurements as in Table 1.

The chelicerae (Fig. 3), typical of the Buthidae, are also depicted on Fig. 9. They resemble those of similar-sized nymphs of the widespread Neotropical scorpion, *C. gracilis* (Gervais 1841) (Figs. 4, 5). The pedipalp patella venter shows several pits that are interpreted as sites of microsetae (Figs. 6, 10). Examination of these two structures definitely eliminated the possibility that the scorpion was a vaejovid. *Centruroides beynai* has similar pits on the pedipalp patella dorsum whose interpretation has varied (Armas 1982; Armas & Marcano Fondeur 1987; Schawaller 1979; Santiago-Blay 1990).

However, the presence of what appears to be submedial mesosomal keels (Fig. 7) and an apodeme-like structure on the prosomal sternum (Fig. 8) is puzzling. Some buthids mature at relatively earlier instars, therefore the possibility that this specimen is a small adult, although unlikely, cannot be disregarded (Williams 1987).

This *Centruroides* from Chiapas can be distinguished from *C. beynai* by the pectine teeth number and metasomal ventral keel sculpturation: the latter has 21–24 pectine teeth and smooth ventral keels on metasomal segments II–IV. *Rhopalurus,* another common Neotropical buthid genus with supernumerary pedipalp finger granules, has a different arrangement of trichobothria db and et (Fig. 11), relatively longer metasomal segments, and lacks a definite Λ-shaped (= inverted V) sulcus flanking a slightly raised portion of mesosomal sternite III. The current knowledge of the *Centruroides* fauna of the region precludes us from distinguishing this specimen from many of its extant congenerics.

Since 1987, the authors have been accumulating morphometric data on fossil scorpions preserved in amber and hope to create a data base that will ease identifications, particularly when only parts of specimens have been preserved. The present specimen is maintained in the private collection of Dr. Rodolfo Molina.

Table 1.—Measurements of fossil *Centruroides*? sp. from Chiapas (México) amber. All measurements in mm. Some measurements could not be obtained because of positioning of the specimen in the piece.

Character	Measurements (mm)
Prosoma	
Carapace	
Anterior, median, posterior widths	1.0, 1.5, 2.3
Diad width	0.4
Median, diad-front margin length	2.0, 0.8
Chelicera	
Basal piece width, fixed finger lengths	1.4, 0.2
Pedipalp	
Femur length, width	1.9, 0.5
Patella length, width	2.5, 0.6
Palm length, width	1.1, 0.5, 2.3
Palm underhand, movable finger lengths	0.9, 2.2
Sternum	
Length, anterior, posterior widths	0.6, 0.2, 0.5
Mesosoma	
Terga	
I length, width	0.3, 2.0
II length, width	0.4, 1.9
III length, width	0.5, 2.2
IV length, width	0.6, 2.4
V length, width	0.7, 2.3
VI length, width	0.6, 2.0
VII length, anterior, posterior widths	1.0, 2.1, 1.0
Overall length	3.7
Metasoma	
Segments	
I length, width	1.5, 1.0
II length, width	1.8, 1.0
III length, width	1.9, 1.0
IV length, width	2.3, 1.0
V length, width, depth	1.9, 0.7, 0.8
Telson	
Vesicle length, depth	0.9, 0.4
Aculeus length	0.1
Total length	17.1

Author GOP can be contacted for further information on the piece.

We thank Stanley C. Williams and Vince F. Lee (Department of Entomology, California Academy of Sciences, San Francisco) for offering suggestions on an earlier version of the typescript and for helpful discussions with author JASB. Grateful appreciation is extended to Dr. R. Molina who brought the specimen to Berkeley for study.

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THE FEMALE OF *GALLIENIELLA BETROKA* (ARANEAE, GALLIENIELLIDAE)

The spider genus *Gallieniella* is known only from Madagascar and the Comoro Islands. Four species have been described (Platnick 1984), but two of them, *G. blanci* and *G. betroka*, have been known only from males. Through the courtesy of Dr. Hubert Höfer of the Landessammlungen für Naturkunde de Karlsruhe, Germany (LNK), I've recently been able to examine a fine series of *G. betroka* that includes the first known females of the species, described below (in the format used in the revision). I thank Dr. Mohammad U. Shadab of the American Museum of Natural History for providing the illustrations.

Gallieniella betroka Platnick
Figs. 1, 2

Gallieniella betroka Platnick, 1984: 10.

Diagnosis.—Females can easily be distinguished from those of *G. mygaloides* Millot and *G. jocquei* Platnick by having epigynal ducts situated anteriorly of the spermathecae (Figs. 1, 2).

Male.—Described by Platnick (1984).

Female.—As in male, except for the following. Total length, not including chelicerae, 4.91 mm. Carapace 2.06 long, 1.69 wide. Femur II 1.49 wide. Eye sizes and interdistances: AME 0.07, ALE 0.07, PME 0.06, PLE 0.06; AME-AME 0.09, AME-ALE 0.02, PME-PME 0.15, PME-PLE 0.05, ALE-PLE 0.07; MOQ length 0.20, front width 0.23, back width 0.28. Clypeal height at AME only slightly greater than their diameter. Chelicerae extending forward distance about three-fifths of carapace length, without ventral tubercle on fang; white scales restricted to pars thoracica. Leg spination: tibia IV v2-3-2. Femur I with lateral stripes more obvious than on femur II. Epigynal ducts relatively long (Figs. 1, 2).

Material Examined.-MADAGASCAR: **Tuléar:** Forêt de Kirindy, Morondava, March 5–19, 1990 (LNK), 2♂, 2♀; Trockenwald, Morondava, March 7–15, 1991, pitfall trap (Butterweck, Petzold, LNK), 2♂, 2♀.

Distribution.—Known only from southern Madagascar.

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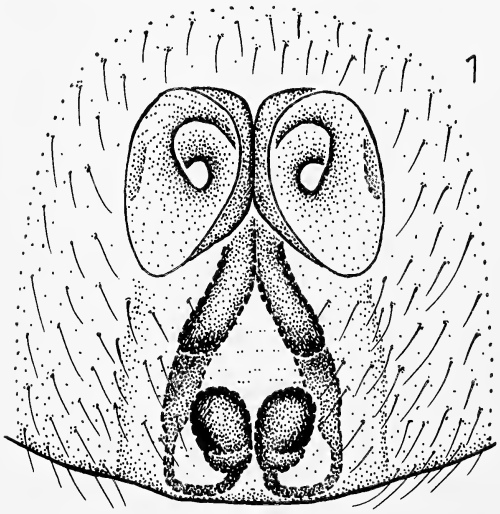

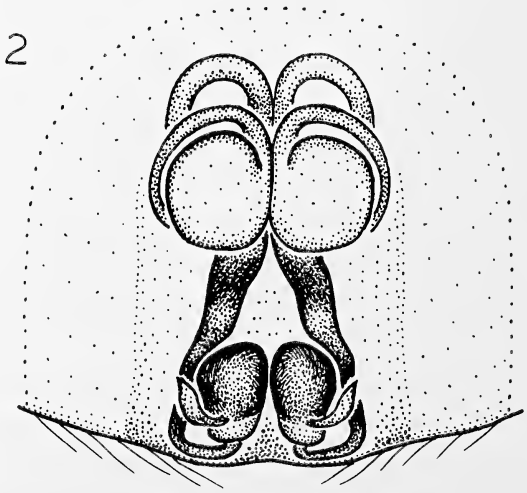

Figures 1, 2.—*Gallieniella betroka* Platnick, female, epigynum: 1, ventral view; 2, dorsal view.

1993. The Journal of Arachnology 21:153–155

NATURAL HISTORY NOTES ON THE HUNTSMAN SPIDER *HOLCONIA IMMANIS* (ARANEAE, HETEROPODIDAE)

Our ecological knowledge of huntsman spiders of the family Heteropodidae is very limited. Even the taxonomy of this family has been worked out poorly. The last complete revision dates back to Hogg (1903). The recently resurrected genus *Holconia* ranges over most of mainland Australia (Hirst 1990), and *Holconia immanis* (Koch) is found in eastern Australia from Queensland to Victoria. *H. immanis* is a large spider: males attain a body length of 30 mm, and females one of 47 mm (Mascord 1970).

New observations of this species were made during a population ecological study of the arboreal gecko *Gehyra variegata* (Duméril & Bibron) (Henle 1990) in Kinchega National Park (32°28′S, 142°20′E), western New South Wales, Australia, from September 1985 to May 1987. Voucher specimens are deposited in the National Insect Collection, Commonwealth Scientific and Industrial Research Organization, Canberra. I thank R. Moran and D. Russell for identification of the spiders.

Gehyra variegata and *H. immanis* were found primarily in black box (*Eucalyptus largiflorens*) riverine woodland on heavy textured cracking clay and in low numbers on a red sand dune covered by hopbush (*Dodonaea attenuata*). In contrast to the abundant gecko, three adult *H. immanis* lived at the huts of Kinchega station in 1986-87. However, several specimens were found on an old brick building at Mt. Wood Station, Sturt National Park. *H. immanis* was not found on river red gum (*E. camaldulensis*) in Kinchega nor at Mt. Wood Station.

Detailed observations on adult females (adults usually determined by size alone: body length > 30 mm) were made in a 150 × 100 m study plot in riverine woodland with 41 widely spaced black box trees. *H. immanis* and *G. variegata* use the same microhabitat. They were found primarily on the trunks of trees or on large branches. The correlation of the number of adult females seen per tree with eight microhabitat variables (height, diameter, number of trunks, leaf area index, number of potential retreat sides, distance to the next tree, food availability, and number of *G. variegata* seen – see Henle [1990] for details of methods) was tested. None of the product-moment-correlations ($-0.16 \leq r \leq 0.40$) was significant (all $\alpha > 0.05$). However, in another more elevated study site of black box riverine woodland, Henle (1990) found a significant correlation of the number of adult female spiders with tree diameter and a marginally significant correlation with tree height and leaf area index. Thus, in this study site, larger trees tend to harbor more specimens.

Both species are typical sit-and-wait foragers. Adult *H. immanis* seem to have 1–2 preferred ambush sites where most individuals were observed on many consecutive nights up to a period of 6 months. The capture of ten food items was witnessed: 1 Pauropoda, 1 Chilopoda (Fig. 1), 2 Lycosidae, 1 subadult *H. immanis*, 1 Phasmida, 1 Heteroptera, 2 Coleoptera, and 1 Lepidoptera. The size of the prey ranged from approximately 0.75 cm to > 10 cm. One unsuccesful predation attempt on a juvenile *Gehyra variegata* was observed. The gecko was not pursued for more than 2–3 cm.

Active specimens were found in all months between September and May. They were inactive in July and August. The recapture of marked specimens showed that *H. immanis* overwinters as adults as is the case in *Clubiona robusta* (Koch) of South Australia (Austin 1984) but contrasts to spiders of colder climates in the Northern Hemisphere which overwinter mainly as eggs (Turnbull 1973).

In September and November 1986 and January 1987, a mark-recapture study was undertaken in the 150 × 100 m study plot. Adult females (body length > 30 mm) were marked on different legs with two colors of nail paint. The marking was visible at least for three weeks, sometimes for two months, and lasted through hibernation (four months). The mark-recapture data of 10 consecutive days were fitted to the geometric and the Poisson distributions (Caughley 1980). The fit to the Poisson distribution was

Figure 1.—*Holconia immanis* preying upon a large centipede.

poor in all three cases ($\chi^2 > 1.949$; $\alpha < 0.2$) while the geometric distribution fitted the data well ($\chi^2 < 0.218$; $\alpha > 0.5$). Thus, the geometric distribution was used to estimate population size. Confidence intervals (CI) were calculated according to Henle (1983). The estimated number of adult female *H. immanis* was 35 (95%–CI: 26–45), 22 (95%–CI: 14–30), and 19 (95%–CI: 11–27) for September 1986, November 1986, and January 1987, respectively. Thus, there appears to have been considerable mortality of adult females between September and November 1986. The mortality of approximately 50% during four months suggests that adult females live for approximately 4–16 months. Miller & Miller (1991) found a similar yearly survivorship of *Geolycosa turricola* (Treat). Only two of the 47 marked individuals with a size of ≥ 3 cm changed the tree of original capture and moved 30 m and 15 m within two and three days, respectively.

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MATING BIOLOGY RESOLVES TRICHOTOMY FOR CHELIFEROID PSEUDOSCORPIONS (PSEUDOSCORPIONIDA, CHELIFEROIDEA)

Mating behavior and spermatophore morphology have provided phylogenetically useful information for both vertebrate and invertebrate taxa (*e. g.*, Proctor 1992a; Alberti *et al.* 1991; Prum 1990). However, because they are transitory phenomena that cannot be observed in preserved specimens, behavior and fragile ejaculates are seldom employed in phylogenetic studies. This is unfortunate because they often contain characters potentially helpful for resolving po-

Table 1.—Spermatophore morphology, mating behavior and male morphology in cheliferoid pseudoscorpions. (+) = character present; (−) = character absent.

		Characters				
Family	Species	Spermatophore droplet	♂ pulls ♀ over spermatophore	Ram's horn organs	♂ pushes sperm in ♀'s genital opening	Reference
Chernetidae	*Epactiochernes tumidus* (Banks)	+	+	−	−	Weygoldt 1966a
	Chernes cimicoides (Fabricius)	+	+	−	−	Weygoldt 1966b
	Dendrochernes morosus (Banks)	+	+	−	−	Weygoldt 1970
	Lustrochernes pennsylvanicus (Ellingsen)	+	+	−	−	Weygoldt 1970
	Americhernes oblongus (Say)	+	+	−	−	Weygoldt 1970
	Parachernes litoralis Muchmore & Alteri	+	+	−	−	Weygoldt 1970
Cheliferidae	*Dactylochelifer latreillei* (Leach)	+	−	+	+	Weygoldt 1966b
	Chelifer cancroides (Linnaeus)	+	−	+	+	Weygoldt 1966b
	Rhacochelifer disjunctus (Koch)	+	−	+	+	Weygoldt 1970
	Hysterochelifer meridianus (Koch)	+	−	+	+	Weygoldt 1970
	Hysterochelifer tuberculatus (Lucas)	+	−	+	+	Weygoldt 1970
	Parachelifer superbus Hoff	+	−	+	+	Weygoldt 1970
Atemnidae	*Paratemnoides braunsi* (Tullgren)	−	+	−	−	Weygoldt 1970
	Atemnus politus (Simon)	−	+	−	−	Weygoldt 1969a
Withiidae	*Withius subpiger* Simon	−	+	−	−	Weygoldt 1969b

lychotomies that have proven intractable to traditional morphological approaches. As well, unlike the usual alternatives of electrophoretic or DNA analyses, characters resulting from studies of mating biology are evolutionarily interesting in themselves.

Because of the diversity of sperm transfer behavior and spermatophore morphology present in pseudoscorpions (Weygoldt 1969a), this group is likely to respond well to phylogenetic resolution using mating characters. In his recent cladistic study, Harvey (1992) ascribed two reproductive synapomorphies to the superfamily Cheliferoidea: production of spermatophores with complex rather than simple sperm masses and transfer of sperm during mating dances rather than without pairing between the sexes. Within the Cheliferoidea, the families Cheliferidae, Chernetidae and Atemnidae were differentiated from the Withiidae by synapomorphies of leg morphology; however, Harvey found no characters to resolve the trichotomy formed by the first three families. In recent literature reviews (Proctor 1992b) I turned up several features of cheliferoid mating biology that both help to resolve this trichotomy and suggest adaptive scenarios for the evolution of mating behavior in this superfamily.

Table 1 lists characteristics of spermatophore morphology, male anatomy and mating behavior for species in the four families of the Cheliferoidea. Spermatophore stalks of the Chernetidae and Cheliferidae apomorphically possess a large droplet of apparently hypotonic liquid that causes the sperm packet to swell and expel its contents into the female genital atrium (Weygoldt 1975). This synapomorphy allows the Cheliferoidea to be resolved from Harvey's (1992) arrangement of [Withiidae (Cheliferidae + Chernetidae + Atemnidae)] to [Withiidae (Atemnidae (Cheliferidae + Chernetidae))]. Other aspects of mating biology provide phylogenetic and evolutionary insight. Males of the Cheliferidae apomorphically possess genital sacs (ram's horn organs) that are everted after spermatophore deposition to attract the females, presumably through pheromones on their surface (Weygoldt 1969a). Concomitant with the evolution of ram's horn organs is loss of the male behavior of pulling females over spermatophores, which is present in the other three cheliferoid families (Table 1). This suggests that pheromonal attraction of the female replaced physical manipulation in the Cheliferidae and raises the possibility that chemical guidance has some advantage over physical contact for these males (*e. g.*, reduced likelihood of palp damage, greater guarantee of female interest in mating). Another apotypic behavior in the Cheliferidae is the male's use of his forelegs to push sperm into the female genital opening after she has mounted the spermatophore (Table 1); no other cheliferoids do this, although there is often extended contact between male and female after the female takes up sperm (*e. g.*, Weygoldt 1970). Adaptive explanations for these and other reproductive characters will be possible only after studying their effects on male fitness.

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1993. The Journal of Arachnology 21:159–160

BOOK REVIEW

Harvey, M. S. 1991. **Catalogue of the Pseudoscorpionida.** (edited by V. Mahnert). Manchester University Press, Manchester M13 9PL UK (distributed exclusively in the USA and Canada by St. Martin's Press Inc., 175 Fifth Avenue, New York, New York 10010 USA). vi + 726 pages. Price $200.00.

It is a pleasure to write about a book which I use almost every day, an indispensable tool for the pseudoscorpion taxonomist. Both the author and the editor deserve many thanks for a job well done.

Harvey's *Catalogue* is the first comprehensive work on the pseudoscorpions of the world since the monographs of Beier (1932a, b) and the lists of Roewer (1937, 1940). Only its Bibliography has a modern counterpart in the bibliography of Schawaller (1980).

An Introduction in three languages (English, French, and German) explains the organization of the book, the systematic treatment of the included taxa, and the limited number of taxonomic changes that have been introduced. It is revealed that 22 families, 434 genera, 3064 species and 169 subspecies of pseudoscorpions are recognized.

The first working section of the book is the Bibliography of nearly 2700 entries. Most references deal with systematic matters, but other aspects of pseudoscorpion biology are included as well, such as behavior, biogeography, ecology, histology, morphology, reproduction, development and life history. The list of publications covers the years from 1758–1988, with a few references to papers published in 1989–90. As far as I have found, very few references to specific pseudoscorpions have been omitted, none of great importance. A valuable feature of the entries is the citation of the names of journals in full – none of the tricky abbreviations which often prove difficult to track down.

The catalogue itself is in the form of a list of all valid species (including fossils) through 1988 (plus a few later ones). The taxonomic arrangement follows a recommendation by me (1982) to forego subordinal groupings and treat only superfamilies. The arrangement of the superfamilies is essentially that of Chamberlin (1931) and Beier (1932a, b), except that the Feaelloidea are placed near the Chthonioidea because of perceived relationships. Within each superfamily the families are listed alphabetically, as are the genera in each family and the species and subspecies in each genus.

Each taxon is documented by a complete synonymy, including reference to papers cited in the Bibliography, with relevant pages and (for species) figures. As the bibliography is essentially complete, so the synonymies are essentially complete. These synonymies can serve to change the shape of papers on pseudoscorpion taxonomy from this time on. No longer will long synonymies be needed for each known species treated when a simple "for synonymy see Harvey 1991" will do.

For each genus, the type species is noted; and for each species, the type locality and reported distribution are given. In a future edition, valuable additions would be the mention, where possible, of the depository of the type specimen(s) of each species and the sex(es) known for each. Some of this information will be difficult or impossible to obtain, but it would be good to begin accumulating such data.

Following the list of those he considered valid species, Harvey presents a list of *nomina dubia* and *nomina nuda*. Included here are two genus-group names and 45 species-group names. In addition, two forms and one variety are mentioned. Then follows a summary of taxonomic changes introduced in the body of the catalogue, including five replacement names, six new type species, five new synonymies, and 101 new combinations.

The Index includes all names appearing in the text. Family-group names and junior synonyms, junior homonyms, *nomina dubia*, and *nomina nuda* are distinguished by differences in typeface. The genus in which a species was originally described is clearly indicated.

Altogether, this is a very valuable book, comprehensive in content and easy to use. It is absolutely required for the pseudoscorpion taxonomist and should be consulted by anyone dealing with any aspect of the biology of these animals. The price of $200 is a bit steep, but for one (or

a group) who is seriously interested in pseudoscorpions, this catalogue will be worth every penny.

Unfortunately, the *Catalogue* will not remain current for long. Already, Harvey (1992, 1993) has introduced changes in the systematics of the Pseudoscorpionida which will necessitate major rearrangement of some families and genera. Other workers will, undoubtedly, be stimulated into action by Harvey's ideas, and amendment of this edition will soon be required.

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Manuscript received 26 April 1993.

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Krafft, B. 1982. The significance and complexity of communication in spiders. Pp. 15-66, *In* Spider Communications: Mechanisms and Ecological Significance. (P. N. Witt & J. S. Rovner, eds.). Princeton University Press, Princeton, New Jersey.

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Figures 1–4.—*A-us x-us,* male from Timbuktu: 1. left leg; 2. right chelicera; 3. dorsal aspect of genitalia; 4. ventral aspect of abdomen.

Figures 27–34.—Right chelicerae of species of *A-us* from Timbuktu: 27, 29, 31, 33. dorsal views; 28, 30, 32, 34, prolateral views of moveable finger; 27, 28. *A-us x-us* holotype male; 33,34. *A-us y-us* male. Scale 1.0 mm.

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CONTENTS

THE JOURNAL OF ARACHNOLOGY

VOLUME 21 **Feature Articles** **NUMBER 2**

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VOLUME 21 1993 NUMBER 3

THE JOURNAL OF ARACHNOLOGY

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Cover illustration: A male *Tetragnatha extensa* from Carlisle, Massachusetts. Original color photo by Joe Warfel of Arlington, Mass. Photograph made with a handheld Olympus OM-1 35mm camera, macro lens, telescoping extension tube and manual flash.

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ULTRASTRUCTURE OF CRIBELLATE SILK OF NINE SPECIES IN EIGHT FAMILIES AND POSSIBLE TAXONOMIC IMPLICATIONS (ARANEAE: AMAUROBIIDAE, DEINOPIDAE, DESIDAE, DICTYNIDAE, FILISTATIDAE, HYPOCHILIDAE, STIPHIDIIDAE, TENGELLIDAE)

William Eberhard: Smithsonian Tropical Research Institute, and Escuela de Biología, Universidad de Costa Rica; Cuidad Universitaria, Costa Rica

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ABSTRACT. The ultrastructure of cribellum silk and associated fibers is described for nine species in eight families, and data from studies of 22 other species are summarized. Possible synapomorphies for filistatids (flattened cribellum fibers), for all cribellates other than hypochilids + filistatids (nodules on cribellum fibers), for deinopids + uloborids + dictynids, and for uloborids + dictynids (loss of reserve warp fibers) are described. Filistatid silk is distinctive and especially complex, and the spatial arrangement of different components is described for the first time.

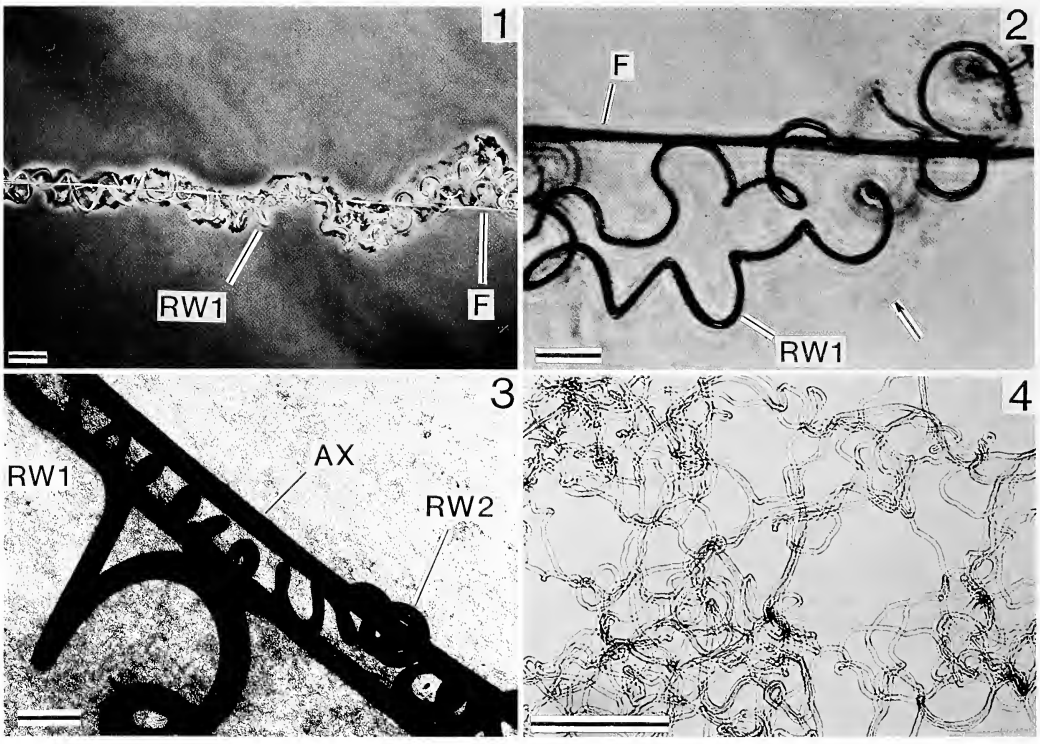
RESUMEN. Se describe la ultraestructura de la seda del cribelo y las fibras asociadas con ella de nueve especies en ocho familias, y se resumen además los datos de 22 otras especies. Se destacan posibles sinapomorfias para filistatidos, para todos los cribelados menos hypochilidos y filistatidos, para dinopidos + uloboridos + dictynidos, y para uloboridos + dictynidos. La seda de los filistatidos es especialmente distinctiva, y la ubicación espacial de los diferentes componentes de ella se describe por primera vez.

Nonviscous adhesive silk is produced by cribellate and some sicariid spiders. The ultrastructure of this silk and the lines associated with it have been described in six different families (Filistatidae, Uloboridae, Deinopidae, Eresidae, Oecobiidae, and Amaurobiidae), using both the light microscope and the scanning and transmission electron microscopes (Comstock 1948; Lehmensick & Kullmann 1957; Friedrich & Langer 1969; Kullmann 1970, 1975; Zimmermann 1975; Opell 1979, 1989a; Peters 1987, 1992a-c). This paper describes the cribellum silk and associated lines of species in five additional families, Desidae, Dictynidae, Hypochilidae, Stiphidiidae, and Tengellidae, and from additional species of Amaurobiidae, Deinopidae, Filistatidae and Uloboridae. We review data on the distribution of several characteristics of cribellum fibers and associated lines. Some characters are apparently consistent within taxonomic groups, and may be useful in systematic studies.

METHODS

No single technique is adequate for studying the complex arrays of fine fibers and lines in cribellate adhesive threads. The light microscope is incapable of resolving finer fibers, while the harsh preparation techniques and observation conditions of both the transmission electron microscope (TEM) and the scanning electron microscope can seriously distort arrays of silk (Peters 1987, 1992a). Both light microscope and TEM were used in the present study.

Silk was collected in the field from webs of mature or nearly mature females, using microscope slides to which three or four square plexiglass rods had been glued (Opell 1989b). The upper surface of each rod was covered with double-sided sticky tape. The web was pressed against the tape, taking care to minimize stress on threads between the rods, and scissors were used to cut the threads connecting the sample to the rest of



Figures 1–4.—Mature female *Hypochilus thorelli*: 1, Mass of cribellum fibrils (barely visible) and highly coiled primary reserve warp (RW1) laid on a foundation line (F) (light microscope); 2, same, with arrow showing edge of cloud of cribellum fibrils (light microscope); 3, one pair of straight axial lines (AX) and two highly curled reserve warp lines of different diameters (RW1, RW2), with fibrils in the background (TEM); 4, cylindrical cribellum fibrils lacking nodules (TEM). Note that fibril diameters do not vary along their lengths (compare with Fig. 9 of *Kukulcania*). Scale lines are, respectively, 50μ, 20μ, 2.6μ, and 0.5μ.

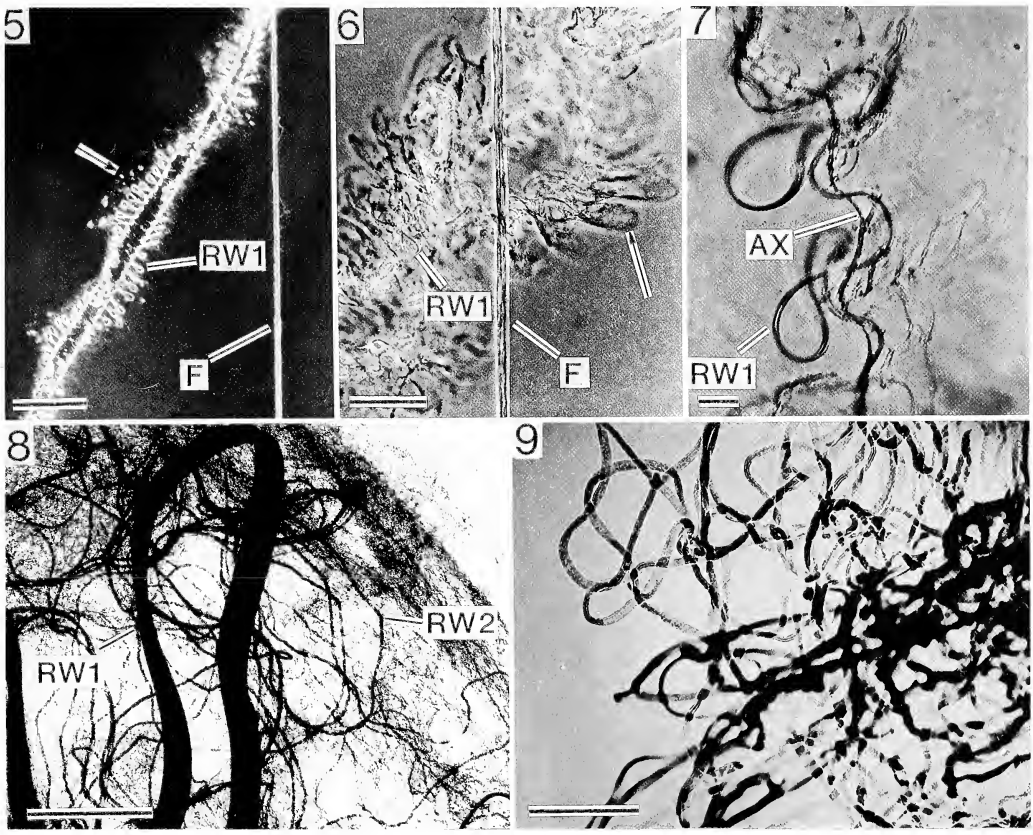
the web. Most observations with the light microscope were made on these slides.

Samples of silk for TEM study were carefully placed on untreated grids under a dissecting microscope, taking care to avoid stressing threads. None of the silk samples were coated or treated in any way before being examined. The silk of *Hyptiotes thorelli* Marx had been stored in sealed containers for 2–3 years; that of the other species was fresher (less than about six weeks old).

The terms "fiber" and "fibril" are used for the smallest units of silk (single cylinders); "line" refers to a combination of fibers of the same type running in parallel; "thread" and "band" refer to combinations of fibers and lines of different types. "Cribellum fibers" are presumed to emerge from the cribellum, while "cribellate" lines and threads ("calamistrated strands" of Peters 1987) contain cribellum fibers as well as other lines that presumably emerge from other spinnerets.

Terminology for different types of fibers and lines follows that of Peters (1987), with the exception that we have used the earlier, functionally descriptive term "reserve warp fibers" of Kullmann (1975) for the highly curled or undulating thicker fibers often associated with cribellum fibrils ("undulating fibers" and "U-fibers" of Peters 1987, 1992a). Identifications of different lines were based only on the morphology and location of the lines, so homologies are thus tentative. A straight or nearly straight fiber running in a pair (except when two separate cribellate threads were laid by a spider with a divided cribellum) in the midst of a mat of cribellum fibers was termed an axial fiber; curled fibers always in the midst of cribellum fibers, also generally in pairs, were termed reserve warp. Information on the glandular origins of different fibers, the spigots from which they emerge (e. g., Peters 1984, 1992a), and their chemical properties will be needed to establish more certain homologies.

Voucher specimens of the spiders are deposited in the Museum of Comparative Zoology,



Figures 5–9.—Mature female *Kukulcania hibernalis*: 5, a pair of highly coiled primary reserve warp lines (RW1) and cribellum silk (barely visible) near a foundation line (F) to which they were attached (light microscope); 6, scalloped edge of mass of cribellum silk (arrow), primary reserve warp (RW1) and foundation line (F) composed of multiple fibers (light microscope); 7, "crinkled" axial line (AX) and primary reserve warp (RW1) in mass of cribellum fibrils (barely visible) (light microscope); 8, flattened primary reserve warp line (RW1) (note variation in diameter) and thinner secondary reserve warp lines (RW2) in mass of cribellum fibrils (TEM); 9, flattened cribellum fibrils (note that apparent diameters change where lines are folded (TEM). Scale lines are, respectively, 200μ, 100μ, 10μ , 5μ , and 0.3μ.

Cambridge, Massachusetts 02138. Collection sites for different genera were the following: *Hypochilus* - near Cullowhee, North Carolina, USA; *Kulkania*, *Tengella*, and *Dictyna* - near San Antonio de Escazu, Costa Rica; *Badumna* and *Paramatachia* - Lamington National Park, SW of Brisbane, Queensland, Australia; *Avella* and *Mahura* - Cape Tribulation, N of Cairns, Queensland, Australia; and *Stiphidium* - Gilles Highway W of Cairns near maximum elevation on way to Atherton, Queensland, Australia.

RESULTS

Table 1 summarizes our observations and those of other authors. More detailed descriptions of the species we studied follow.

Hypochilus thorelli Marx (Hypochilidae)—Observations with the light microscope revealed a more or less cylindrical mass of cribellum silk associated with a pair of linear axial fibers plus a pair of moderately coiled reserve-warp fibers (Figs. 1, 2). Additional, thinner secondary reserve warp fibers were revealed with the TEM (Fig. 3). The fibrils of cribellum silk were apparently cylindrical, and lacked nodules (Fig. 4).

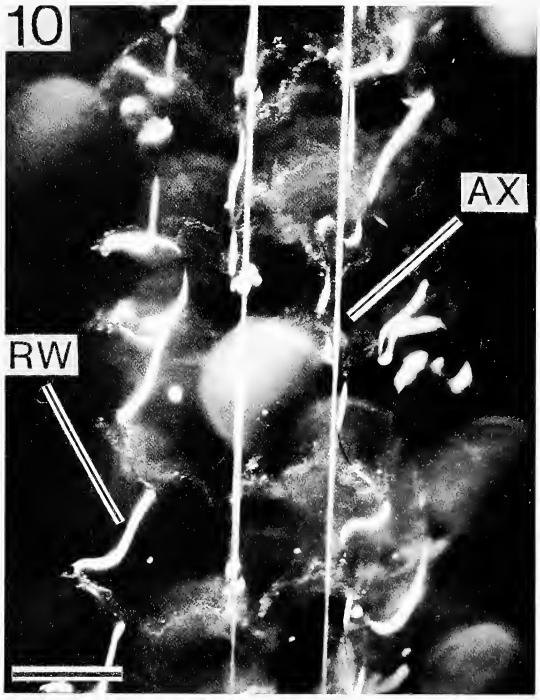
Kukulcania hibernalis (Hentz) (Filistatidae)—The band of cribellate silk was laid along a thick foundation line (Figs. 5, 6), to which it was attached periodically. The foundation line had multiple grooves (Fig. 6), suggesting it was composed of many different strands. The silk of the foundation line was unusual in being relatively rigid: when cut, the line did not sag or fold. The

Table 1.—Characteristics of cribellum silk and associated lines in 31 species of spider. (a) Type of microscope: LM = light microscope; TEM = transmission electron microscope; SEM = scanning electron microscope. (b) Fibrils: C = cylindrical fibril; R = flattened, ribbonlike fibril; N = nodules along fibril. (c) Number of pairs of lines. (cc) C = cylindrical lines; R = flattened fibers. (d) Thick lines of two different diameters present in photo, but their arrangement (coiled, straight, etc.) unknown. (e) Opell 1979. (f) Eberhard 1972 for building behavior. (h) Eberhard 1982 for building behavior. (i) No direct observations, but builds typical orb—Wiehle 1928. (j) Marples & Marples 1937 for building behavior. (l) No direct observations, but spider spins typical orb—Opell 1987. (m) Coddington 1986. (n) Eberhard unpubl. (o) Eberhard unpubl. (p) Inclusion of this genus in Amaurobiidae is somewhat uncertain—R. Forster pers. commun.

Taxon	Type of microscope (a)	Fibrils (b)	Foundation line	Reserve warp (c)	Reserve warp (cc)	Axiall lines?	Puffs?	References
Hypochilidae								
Hypochilus thorelli	LM, TEM	C	?	≥2		yes	no	this study
Filistatidae								
Filistata insidiatrix	LM, TEM	R	Yes	1	C	yes?	no	Lehmensick & Kullman 1956; Peters 1987
Kukulcania arizonicus	TEM	R	?	≥2? (d)		?	?	Friedrich & Langer 1969
K. hibernalis	LM, TEM	R	yes	≥2?	R	yes? (2)	no	Comstock 1948; this study
Uloboridae								
Zosis plumipes	TEM	C + N	no (e)	?		?	?	Peters 1987
Uloborus diversus	LM, TEM	C + N	no (f)	0		yes	yes	Friedrich & Langer 1969
U. walckenaerius	LM, TEM	C + N	no	0		yes	yes	Peters 1987
U. penicillatus	SEM, TEM	C + N	no (h)	?		yes	yes	Opell 1979
U. plumipes	LM, TEM	C + N	no (i)	0		yes	yes	Peters 1984
U. sp. (Cairns, Aust.)	LM		no	0		yes	yes	this study
Polenecia producta	LM	C + N	yes	0		yes	yes?	Peters 1983, 1987
Miagrammopes sp.	LM	C + N	yes	0		yes	yes	Peters 1987
M. animotus	LM, SEM	?	yes	0		yes	yes	Opell 1989b
Hyptiotes paradoxus	LM, SEM	C + N	no (j)	0		yes	yes	Lehmensick & Kullmann 1956
H. cavatus	SEM	?	no (k)	?		yes	yes	Opell, Roth, & Cushing 1990
Tangaroa beattyi	SEM	?	no? (1)	?		?	yes	Opell 1989b

Table 1.—Continued.

Taxon	Type of microscope (a)	Fibrils (b)	Foundation line	Reserve warp (c)	Reserve warp (cc)	Axial lines?	Puffs?	References
Deinopidae								
Deinopus sp.	SEM	?	no (m)	1		yes	yes	Kullman 1975
D. subrufus	LM, SEM, TEM		no	1		yes	yes	Peters 1992c
Avella sp.	LM, TEM	C + N	no	1	C	yes	yes	this study
Eresidae								
Stegodyphus lineatus	LM	?	no/yes	4		yes	no (?)	Kullmann 1975; Peters 1987, 1992a
S. mimosarum				"several"		yes	?	Kullmann 1970
S. sarasinorum	LM, TEM	?	no (n)	3		yes	no	Kullman 1975
S. dumicola	LM, SEM	?	no/yes	3		yes		Peters 1992a
Seothyra henscheli	LM, TEM, SEM	?	no		C	yes	?	Peters 1992b
Oecobiidae								
Oecobius annulipes	TEM	C + N		1				Zimmerman 1975
Amaurobiidae								
Amaurobius sp.	LM			1 or 2		yes		Comstock 1948
A. sp.	TEM	C + N						Foelix 1982
Mahura sp. (p)	LM, TEM	C + N	no	1	C	no	?	this study
Tengellidae								
Tengella radiata	LM, TEM	C + N	no (o)	2		yes	no	this study
Dictynidae								
Dictyna sp.	LM, TEM	C + N	no/yes	0		no	yes	this study
Stiphidiidae								
Stiphidium sp.	LM, TEM	C + N	no	1	C	yes	no/yes	this study
Desidae								
Badumna sp.	LM, TEM	C + N	no	1		yes	no	this study
Paramatachia decorata	LM, TEM	C + N	yes	0		no	"yes"	this study



Figures 10–11.—Mature female *Tengella radiata*: 10, flat mass of cribellum fibrils (barely visible), with a pair of straight axial lines (AX) and a pair of folded reserve warp lines (RW) (light microscope); 11, cylindrical cribellum fibrils with nodules (TEM). Scale lines are, respectively, 100μ, and 0.5μ.

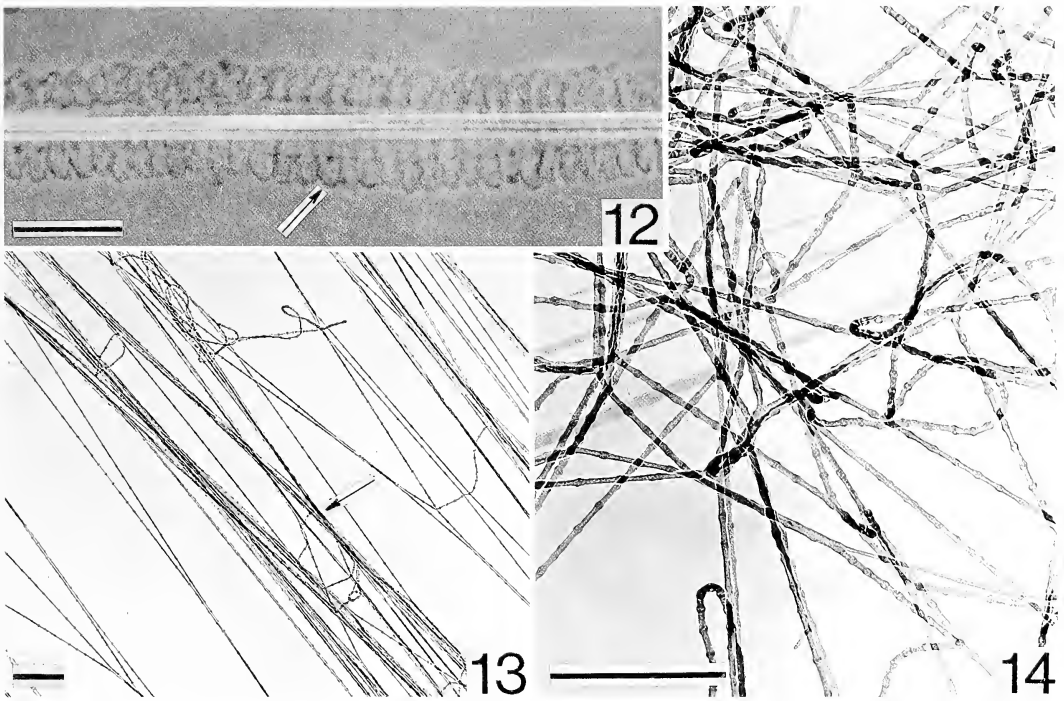
foundation line was laid as the spider moved away from its retreat, and the cribellum silk and associated fibers were laid during the return trip (Eberhard 1988). In some places the band of cribellate silk was more or less linear (Fig. 5), but more often it was piled up or coiled on itself, forming irregular loops.

The internal structure of the band was complex. Under the light microscope a more or less looped and folded pair of helical fibers was seen (the helix is relatively extended in Fig. 5), with the mass of cribellum fibrils visible as a faint cloud (Figs. 5–7). Within each helix, a relatively thick, smooth primary reserve warp fiber was curled in a highly regular fashion that included a series of short, more or less straight basal portions alternating with longer loops (Figs. 5, 7). Each loop was oriented in nearly the same direction as the previous one. The axial line, which was thinner and apparently somewhat crinkled, ran near and approximately parallel to the straight basal portions of the loops of the primary reserve warp fiber (Fig. 7).

Under the TEM, the primary reserve warp proved to be flattened and ribbon-like, rather than cylindrical (Fig. 8). The axial line was seen to consist of a pair of lines, with the "crinkles" consisting of portions where one fiber was curled helically around the other. Additional, finer secondary reserve warp fibers (number uncertain) were folded loosely and irregularly in the area of the loops of primary reserve warp (Fig. 8). The cribellum fibrils were smooth and ribbon-like, rather than cylindrical (Fig. 9). They lacked the nodules seen in the silk of many other species (Table 1).

Tengella radiata (Kulczynski) (Tengellidae)—A more or less flat mat of cribellum silk lay on or around a pair of axial fibers plus a pair of kinked or somewhat curled reserve-warp fibers (Fig. 10) which were produced at the same time as the cribellum silk. The edges of the mat were not regularly scalloped, and the reserve warp fibers appeared to be cylindrical. The mat twisted from side to side as a relatively rigid unit in weak air currents under the light microscope. The fibrils of cribellate silk were apparently cylindrical, with many small nodules scattered along their lengths (Fig. 11).

Dictyna sp. (Dictynidae)—The cribellum silk formed a relatively flat mat with regularly scalloped edges (Fig. 12). In some cases the mat was



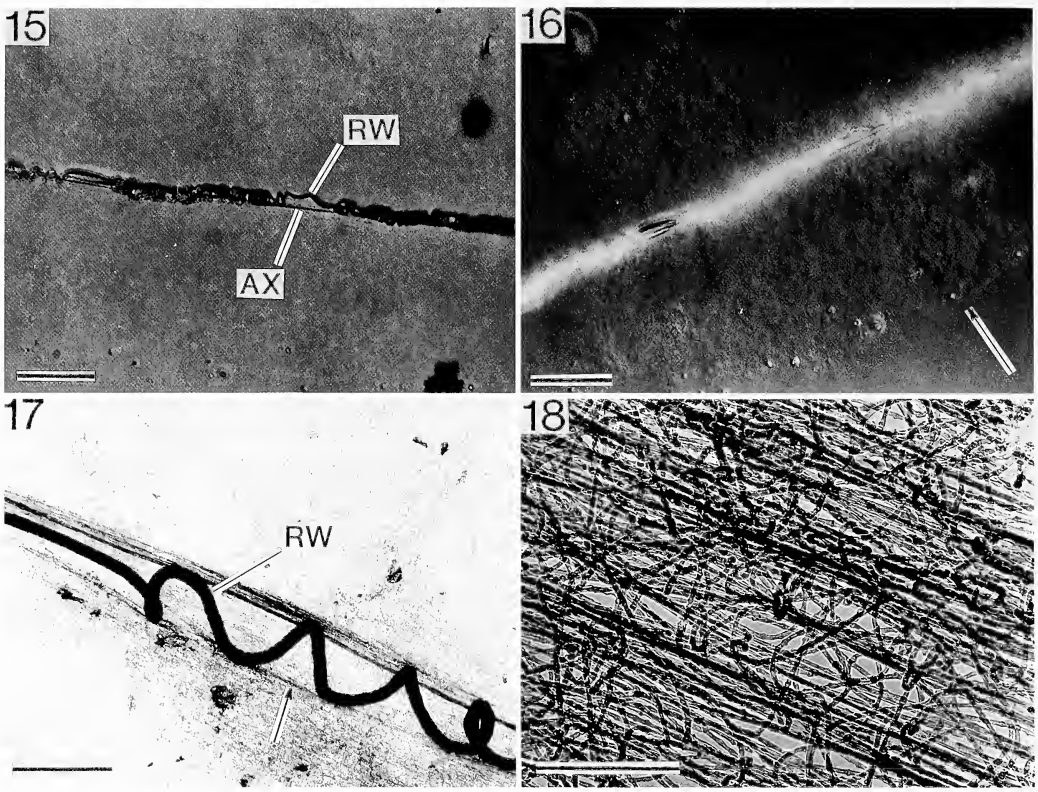
Figures 12–14.—Mature female *Dictyna* sp.: 12, mat of cribellum silk with scalloped edges (arrow) laid along a foundation line (light microscope); 13, cribellum fibrils clumped together in places to form cables (arrow) (TEM); 14, cylindrical cribellum fibrils with nodules (TEM). Scale lines are, respectively, 100μ, 1μ, and 1μ.

laid on a relatively thick foundation line (Fig. 12), while in others there was no foundation line. Careful searches using the TEM showed that there were neither axial nor reserve warp lines. Under the light microscope a pair of darker lines were sometimes visible in the central portion of the mat of cribellum fibers, but these presumably corresponded to cables composed of accumulations of cribellum fibrils (Fig. 13). Cribellum fibrils were cylindrical, with nodules along their length (Fig. 14).

Stiphidium sp. (Stiphidiidae)—The non-planar mass of cribellum fibrils was not laid along a foundation line (Fig. 15), and did not have a regularly scalloped outline (Fig. 16). Associated with the cribellum silk were a pair of straight, apparently cylindrical axial fibers and a pair of curled, cylindrical reserve warp fibers (Figs. 15, 16). The cylindrical reserve warp was curled tightly for short stretches which alternated with stretches of similar lengths in which it was relatively uncurled (Figs. 15–17). The cribellum fibrils were cylindrical, with nodules (Fig. 18).

Badumna sp. (Desidae)—In places two mats of cribellate silk ran in close parallel, presumably the product of the divided cribellum; in other places they were farther apart. The lateral outlines of mats were not regularly scalloped (Fig. 19). Each mat had a straight, relatively thin axial fiber, and a cylindrical reserve warp fiber in which the degree of coiling varied (Figs. 19–21). The cribellum fibrils were cylindrical, with nodules (Fig. 22).

Paramatachia decorata (Dalmas) (Desidae)—The lateral outlines of mats of cribellum silk were often regularly scalloped, although the thickenings ("puffs") often did not occur at the same point on either side of the mat (Fig. 23). Mats of cribellate silk were usually but not always associated with foundation lines (Figs. 24, 25). When viewed with the light microscope a pair of straight axial fibers seemed to be present (Fig. 23), but no reserve warp fibers were seen. In some places the mat of cribellum fibrils was coiled on the axial line. Neither axial nor reserve warp fibers were found using the TEM, however. Over short stretches, cribellum fibrils came together to form cables which gave the false impression of thicker fibers (Fig. 25), but these differed from the axial fibers seen in the light microscope in being only relatively short. It appears that axial fibers were absent from some samples, but it is



Figures 15–18.—Mature female *Stiphidium* sp.: 15, straight axial line (AX) and reserve warp line (RW) with alternating highly curled and straighter regions (light microscope); 16, same, showing non-scalloped edge of mat of cribellum fibrils (arrow) (light microscope); 17, curled cylindrical reserve warp line (RW) with cribellum fibrils, some of which clump together to form cables (arrow) (TEM); 18, cylindrical cribellum fibrils with nodules (TEM). Scale lines are, respectively, 100μ, 100μ, 5μ, and 0.5μ.

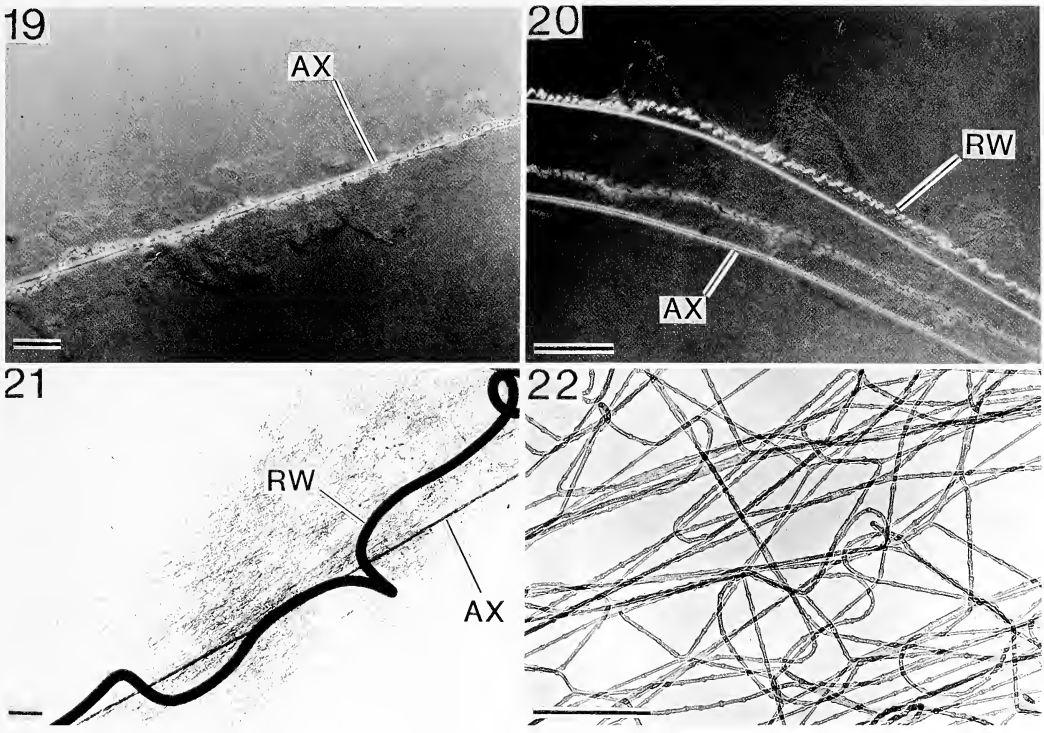
uncertain whether they were present in others. The cribellum fibrils were cylindrical, with nodules (Fig. 26).

Mahura sp. (Amaurobiidae)—Many mats of cribellate silk in the sheet of this spider's web were composed of parallel double bands, presumably due to the divided cribellum. In contrast, mats of cribellate silk in the mesh above the sheet were usually single. Each cribellate mat collected from the sheet had a single cylindrical reserve warp fiber, which was alternately tightly coiled and relatively uncoiled (Fig. 27). Axial fibers were not clearly visible in the light microscope (appearing to be present only in short stretches), and no axial lines were seen with the TEM. In places cribellum fibrils came together to form cables, and presumably these were the "axial fibers" seen in the light microscope. Cribellum fibrils were cylindrical, with nodules (Fig. 28).

Avella sp. (Deinopidae)—The lateral margins of each mat of cribellum silk were strongly scalloped (Fig. 29). A pair of linear axial fibers and a pair of loosely coiled, cylindrical reserve warp fibers ran through the central portion of the mass (Figs. 29, 30). Cribellum fibrils were cylindrical, with nodules (Fig. 31).

DISCUSSION

The data available to date suggest that some ultrastructural characteristics of cribellate capture silk are relatively constant within and between taxa (Table 1). The consistency is especially clear in the cylinder plus nodule structure of cribellum fibrils, and the lack of reserve warp fibers in the best studied family, Uloboridae. It should be born in mind that the changes in cribellum fibril morphology in the TEM (electron bombardment in a vacuum) are not known. Thus the morphology of fibrils described here may differ from that of fibers under normal conditions. The tentative nature of homologies of the lines

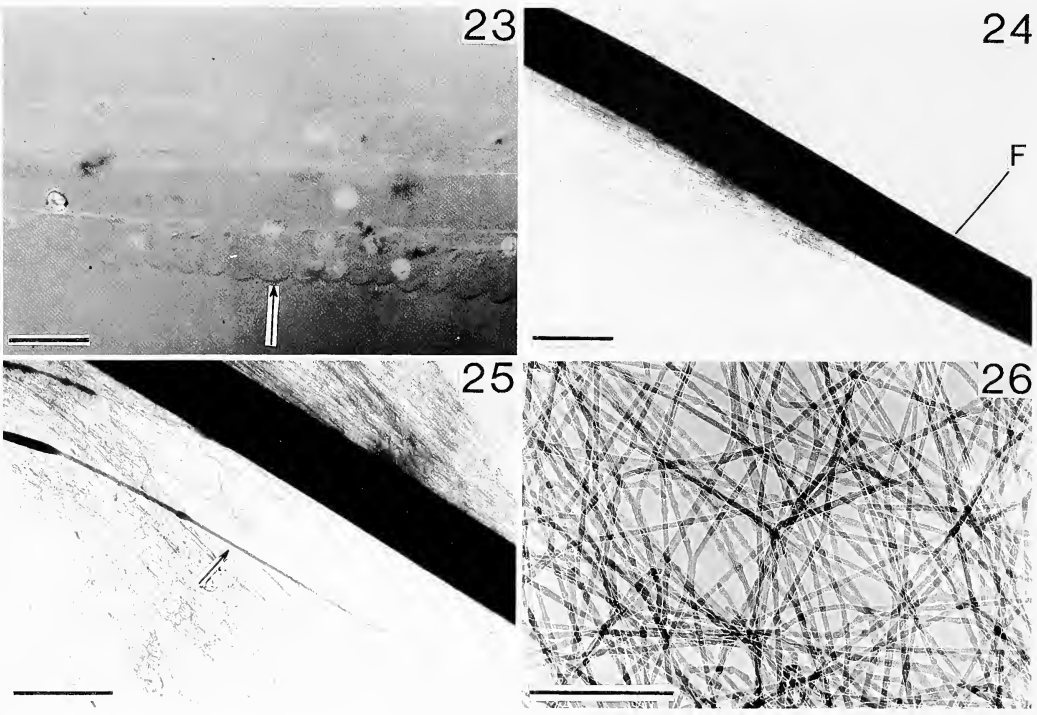


Figures 19–22.—Mature female *Badumna* sp.: 19, mat of cribellum fibrils with irregularly scalloped edges, axial lines (AX), and curled reserve warp line (light microscope); 20, pair of axial lines (AX) and pair of alternately curled and uncurled reserve warp lines (RW), with a more regularly scalloped mat of cribellum fibrils (light microscope); 21, curled cylindrical reserve warp line (RW) and straight axial line (AX) with cribellum fibrils (TEM); 22, cylindrical cribellum fibrils with nodules (TEM). Scale lines are, respectively, 150μ, 100μ, 2μ, and 0.5μ.

associated with cribellum silk should also be kept in mind.

While much more data need to be gathered to determine whether the patterns of distribution will hold up, it may be useful to attempt a tentative comparative analysis. If one superimposes the data on silk ultrastructure on a recently proposed pylogeny of cribellate spiders (Coddington & Levi 1991), several hypotheses result (Fig. 32): 1. Ribbon-like cribellum fibrils are a derived character of filistatids (*Filistata*, *Kukulcania*). 2. Nodules on cribellum fibrils are a synapomorphy linking all cribellates other than filistatids and hypochilids; 3. Lack of "reserve-warp" lines is a derived character, present in the single dictynid, one of the two desids, and all of the 12 uloborids. Since several details of web construction behavior link Uloboridae and Deinopidae (which has reserve warp fibers), the loss either occurred independently in Uloboridae and Dictynidae (Fig. 32) (with subsequent reacquisition of both axial and reserve warp lines in *Badumna* and loss of axial fibers in *Mahura*), or dictynoids are the sister group of uloborids + deinopids, and deinopids and *Badumna* secondarily re-acquired reserve warp lines (with a loss of axial lines in dictynoids and *Mahura*).

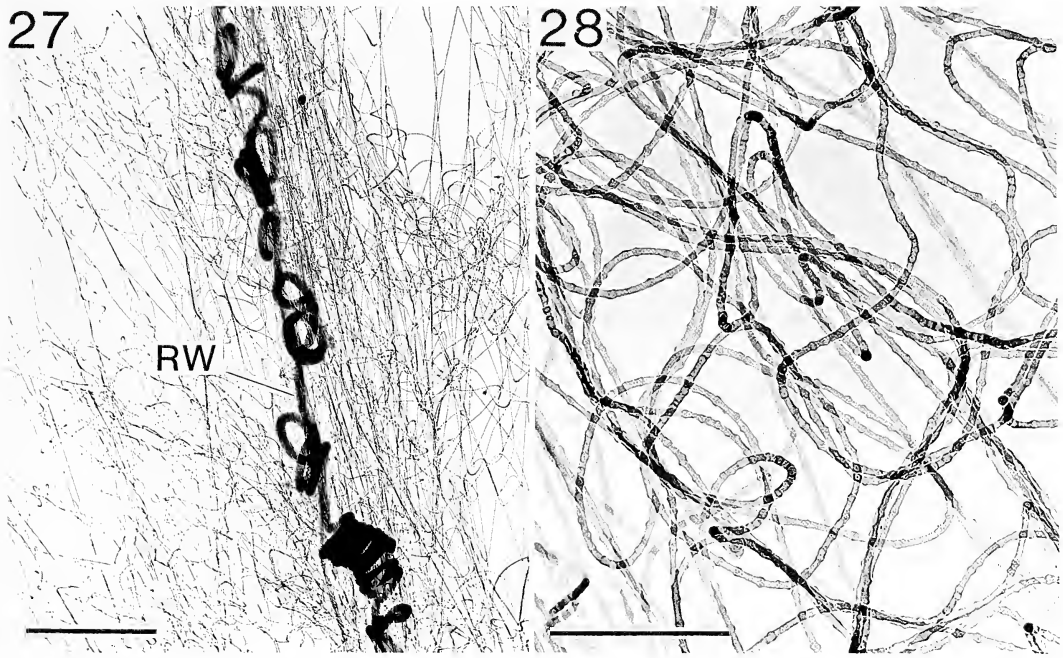
An additional character, noted by other authors, is the scalloped outline of the mass of cribellate silk ("puffs"), which may unite Uloboridae, Deinopidae, Dictynidae and the desid *Paramatachia* (in at least some uloborids, a puff is actually shaped more nearly like a twisted torus). This character may be somewhat less useful, however, since: 1) intermediate degrees of "scalloping" occur (e. g., Figs. 12, 20, 23), and it is not clear how regular scalloping must be to be condsidered a puff; and 2) some uloborid mats are only barely scalloped (Peters 1984, 1987). We were unable to confirm the presence of paracribellar fibrils (Peters 1984, 1987) in any of our species (unless they correspond to the "cables" of cribellum fibrils seen in *Dictyna*, *Paramatachia*, and *Mahura*).



Figures 23–26.—Mature female *Paramatachia decorata*: 23, mat of cribellum silk with scalloped edges (arrow) (apparent axial lines are slightly out of focus except at right and left margens) (light microscope); 24, foundation line (F) to which cribellum silk was attached (note multiple fibers) (TEM); 25, foundation line with cables formed by multiple cribellum fibrils (arrow) (TEM); 26, cylindrical cribellum fibrils with nodules (TEM). Scale lines are, respectively, 100μ, 5μ, 5μ, and 0.5μ.

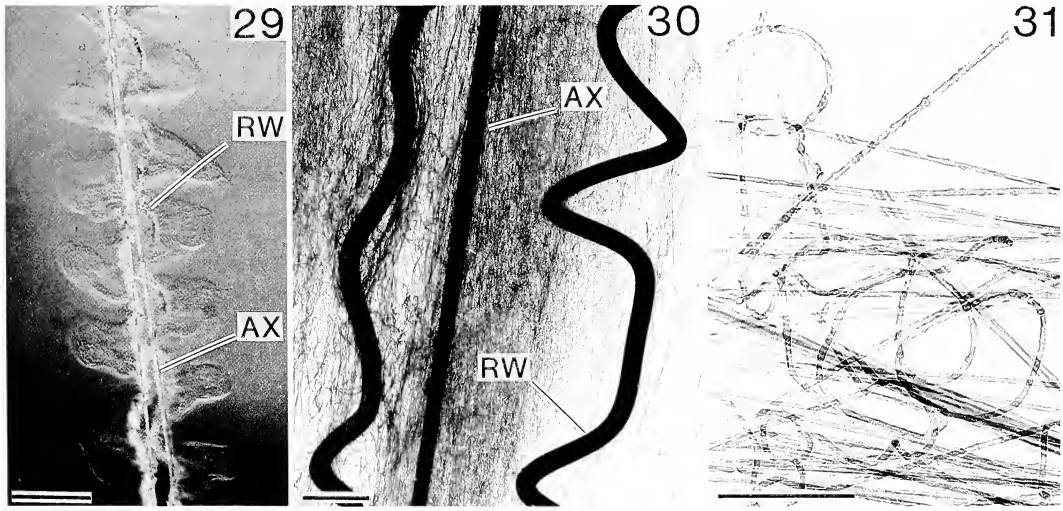
The positions of the fibers associated with cribellum silk help clarify some details of combing behavior. Assuming that spider silk is polymerized by being pulled (e. g., Foelix 1982), the presence of highly curled reserve warp fibers, which are presumably pulled out by strokes of the calamistrum and then fold or coil upon themselves, suggests that cribellum silk *per se* is piled on itself in the sticky threads of all species with curled reserve warp fibers. In some cases the tendency of reserve warp fibers to curl up may even cause clumping to occur. For instance, the secondary helices of *Filistata* and *Kukulcania* may result from curling of the axial fibers and/or the primary reserve warp lines. In species such as *Tengella radiata*, where the reserve warp fibers curl less, they appear to have little influence on the shape of the mass of cribellum fibrils. In both these groups (as well as in *Stegodyphus* - see Eberhard 1988), the spiders do not pull the cribellate silk threads taut in their webs. Rather, silk accumulates and sags free behind the spider as it is combed from the cribellum with the calamistrum. The thread is under no tension other than that resulting from its own weight and friction with air currents, and is actually often piled on itself in *Kukulcania* and *Stegodyphus* webs. Presumably when cribellum fibrils accumulate in this way, the force of adhesion is increased by bringing more silk surface into contact with the prey (Opell 1990). The effective length of the silk is probably also increased, making escape more difficult when the prey attempts to pull away.

Many authors have thought that each of the puffs in a mass of cribellum fibrils is produced by a single combing movement of the calamistrum (Eberhard & Langer 1969; Friedrich & Langer 1969; Opell 1979; Peters 1992c), but Peters (1984) attributed puffs to rhythmic clamping movements of the posterior spinnerets. The presence of many helical turns of reserve warp fibers between each pair of puffs in the sticky threads of *Deinopus* sp. and *Deinopus subrufus* (Kullmann 1975; Peters 1992c), and *Avella* sp. (this study) indicates that the second hypothesis is more likely. The combing movement necessary to produce a puff would be too short to pull out such lengths of reserve warp fiber.



Figures 27–28.—Mature female *Mahura* sp.: 27, reserve warp line (RW) which is more tightly curled in some places than others (TEM); 28, cylindrical cribellum fibrils with nodules (TEM). Scale lines are, respectively, 2μ and 0.5μ.

Similar reasoning indicates that combing movements of the calamistrum in many species are not responsible for pulling out axial fibers. The looped and tangled cribellar fibrils (presumably pulled by the calamistrum) are substantially longer than the axial fibers. Probably many axial fibers are pulled out as the spider moves away from the last attachment point. This mechanism is not possible, however, in spiders such as *K. hibernalis* and *Stegodyphus gregalis*, which do



Figures 29–31.—Mature female *Avella* sp.: 29, highly scalloped mat of cribellum silk with pair of axial lines (AX) and reserve warp lines (RW) (light microscope); 30, axial line (AX) with pair of reserve warp lines (RW) and cribellum fibrils (TEM); 31, cylindrical cribellum fibrils with nodules (TEM). Scale lines are, respectively, 100μ, 5μ, and 0.5μ.

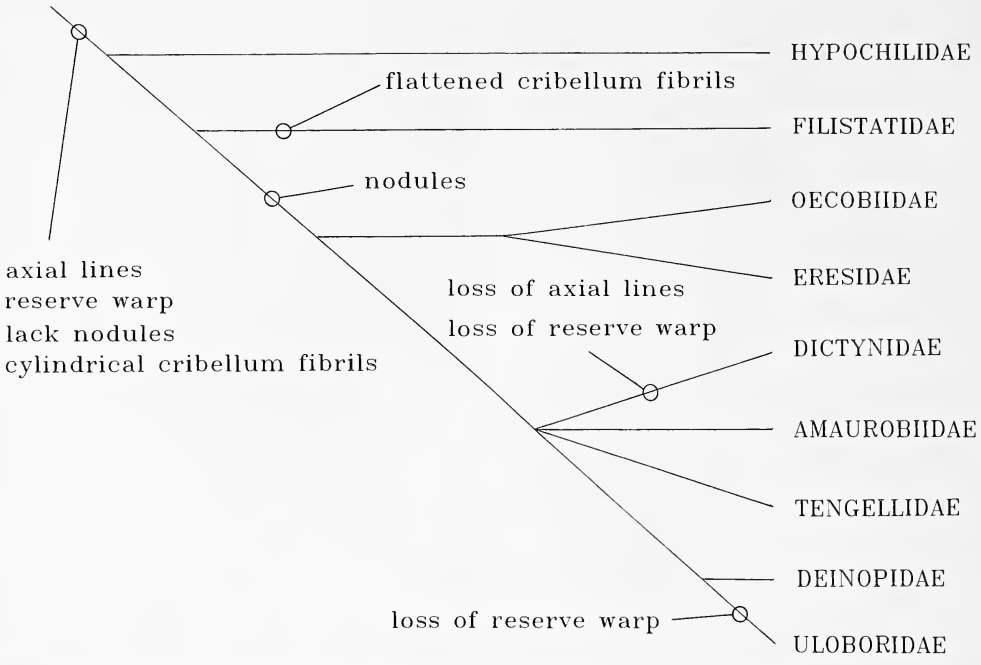


Figure 32.—Phylogeny of the families in which the ultrastructure of cribellum silk and associated lines has been studied (after Coddington & Levi 1991), with data on silk morphology (Table 1) superimposed to show possible transitions.

not move forward during most of the time cribellum silk is being combed (Eberhard 1988; see also Opell 1990 on *Miagrammopes*). It is not clear how axial fibers are pulled from the spinnerets in these species.

Comstock (1948) speculated that the helix of threads (he saw them as loops) of *Kukulcania hibernalis* (under the name *Filistata*) result from movements of the spinnerets, while the very regular loops of the primary reserve warp are made by combing movements of the calamistrum. Given the much longer length of the secondary reserve warp fibers, however, it seems more likely that their irregular folding may be associated with the combing movements of the calamistrum. The highly ordered folding of the primary reserve warp and the helical coiling of the swath itself is presumably due to their intrinsic curliness (but see below), and the fact that spider moves forward very little as it combs out silk, so that cribellate silk "piles up" between attachments to the foundation line.

Comstock also thought that the axial fibers of *K. hibernalis* are highly elastic, stretching "to fifty times their first length". We were unable to confirm this. Instead, when a swath was pulled under the light microscope, a process of sequential breaking occurred (possibly of the axial fibers), bringing the reserve warp fibers under tension as described by Kullmann (1975) for *Stegodyphus*. As the swath was slowly pulled, it extended: the primary reserve warp began to unfold, but did so unevenly, in little starts. It became completely unfolded in some places before others. Eventually the primary reserve warp became completely extended. If the tension was then relaxed, the reserve warp remained extended, and did not recoil to its original position (thus failing to show the intrinsic curliness postulated above). Further extension caused the primary reserve warp fiber to break, and with that the entire thread usually broke. Thus the finer, secondary reserve warp fibers of *K. hibernalis* apparently serve in adhesion (of the cribellum silk to the primary reserve warp? to the prey?) rather than to increase the tensile strength and elongation of the array of lines as do the secondary reserve warp fibers of *Stegodyphus* (Kullmann 1975). Presumably the extension Comstock observed was the extension of the entire array of cribellum silk and associated fibers.

The most complex and distinctive arrays of cribellum silk and associated fibers are those of filistatids. These may show intergeneric differ-

ences. Lehmensick & Kullmann (1956) describe a two-part mass of adhesive silk in *Filistata insidiatrix*, laid in small accumulations on a previously built foundation line, just as in *K. hibernalis*. Although they did not mention that each of the two parts has a helical form, this seems to be the case in the light microscope photo of Peters (1987) of the same species. Lehmensick & Kullmann also noted a pair of axial fibers, which seem (in their light microscope photo, plate 2, fig. 3) to be thicker and straighter than those of *K. hibernalis*. The fiber labelled axial line in their TEM micrograph (plate 2, fig. 4) may, however, may not correspond to the light microscope axial fiber: it does not run through the mass of cribellum fibers and curled reserve-warp fibers; and a thinner fiber, which is more appropiately located and which resembles the axial fiber of *K. hibernalis*, is unlabelled. Perhaps the line they labelled as an axial line in their TEM micrograph was a foundation line.

Also unique to filistatids is the non-cylindrical, ribbon-like form of the primary reserve warp fiber. Judging by the flattened tips of the paracribellar spigots on the posterior median spinnerets of *K. hibernalis* (figs. 56–58 in Platnick et al. 1991), these spigots may be the source of primary reserve warp fibers. This speculation is supported by the existence of a somewhat similar, slit-shaped opening of the "major ampullate gland spigot" on the anterior lateral spinneret of *Loxosceles rufescens* and *L. reclusa* (Platnick et al. 1991), and the fact that *L. rufescens* also makes a wide, ribbon-like band of silk (Lehmensick & Kullmann 1956; Kullmann 1975). It is in apparent conflict with the lack of paracribellar spigots in hypochilids, eresids, and *Tengella* (Platnick et al. 1991). Peters (1992a) has established that reserve warp fibers are secreted from spigots on the posterior median spinnerets in *Stegodyphus*. Further work is needed to establish which spigots produce these and other fibers.

The band-like cribellum fibrils of *K. hibernalis* may be associated with their bladder-shaped "claviform" cribellar spigots (fig. 52 of Platnick et al. 1991), which are quite different from the more sharply-tipped "strobilate" spigots known for other cribellates (Kullmann 1975; Opell 1979; Peters 1984, 1987, 1992; Platnick et al. 1991). A second possible silk-spigot association, between the presence of nodules on cribellum fibrils and nodule-like expansions on the cribellum spigots, is apparently ruled out, however, by the presence of expansions on the spigots of *Hypochilus pococki* (Platnick et al. 1991), and the absence of nodules on the fibrils of *H. thorelli*.

Homologies of the filistatid fibers with those of other species are somewhat uncertain. Comstock (1948) apparently also noted the axial fibers, and both primary and secondary reserve warp fibers in *K. hibernalis* (calling them, respectively, primary looped threads, secondary looped threads, and irregular threads). We have designated as "axial lines" the least folded lines within the helices, but the double nature of these lines is unique. If, instead, the wider, regularly looped "primary reserve warp" fibers are homologous to the axial fibers of other species, the characteristics of *Kukulcania* in Table 1 and the position of filistatids in Fig. 32 would be little altered.

ACKNOWLEDGMENTS

Fred Coyle kindly sent carefully packed samples of *Hypochilus* silk. Herb Levi helped with identifications. Robert Raven facilitated work in Australia. Brent Opell, M. J. West-Eberhard and especially Charles Griswold made helpful comments on preliminary drafts of the manuscript. The Vicerrectoría de Investigación of the Universidad de Costa Rica provided financial support. We thank all for their help.

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STUDIES ON SPECIES OF HOLARCTIC *PARDOSA* GROUPS (ARANEAE, LYCOSIDAE). V. REDESCRIPTION OF *PARDOSA WASATCHENSIS* GERTSCH AND DESCRIPTION OF A NEW SPECIES FROM UTAH

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ABSTRACT. Two North American *Pardosa* species assigned to the *modica* group are treated and illustrated. *Pardosa wasatchensis* Gertsch (Montana, Wyoming, Colorado, Utah, Idaho, Washington; with *Pardosa subra* Chamberlin & Ivie from Oregon placed as junior synonym) is redescribed, and the male is described for the first time. *Pardosa vogelae*, new species, is described on material from Leidy Peak and vicinity in the Uintah Mountains (Utah).

Species of the *modica* group within the wolf spider genus *Pardosa* have previously been treated by Kronestedt (1975, 1981, 1986, 1988) and Dondale & Redner (1990). This paper deals with another two species assigned to this group of species.

Pardosa wasatchensis was described from the female by Gertsch (1933) and since then little has been added to the knowledge of this species, which seems to be restricted to western U. S. (Fig. 22). *P. subra*, described by Chamberlin & Ivie (1942), regrettably also from the female sex only, seems to be conspecific with *P. wasatchensis*. The male of *P. wasatchensis* is described here for the first time.

The new species *Pardosa vogelae* has so far been found only in the eastern parts of the Uintah Mountains of Utah. Whether or not it has a restricted distribution remains to be explored. [This discovery is parallelled by the find at a single locality in Colorado of a high altitude species in the *nigra* group, *P. gothicana* Lowrie & Dondale (1981), calling for more intense studies of Cordilleran *Pardosa*.]

METHODS

Material is deposited in the following collections: AMNH—American Museum of Natural History, New York; BRV—private collection of B. R. Vogel; CNC—Canadian National Collection of Insects and Arachnids, Ottawa; MCZ—Museum of Comparative Zoology, Cambridge, Massachusetts; NRS—Swedish Museum of Natural History, Stockholm (material gratefully donated by D. C. Lowrie and B. R. Vogel).

Terminology and methods of study follow Kronestedt (1975, 1986). Measurements refer to specified individuals. Eyepiece micrometer units (as given for eyes) can be converted to mm by dividing by 80.

Pardosa wasatchensis Gertsch

Figs. 1, 3, 5, 6, 9, 10, 12, 14, 15, 17, 19, 21a, 22; Table 1

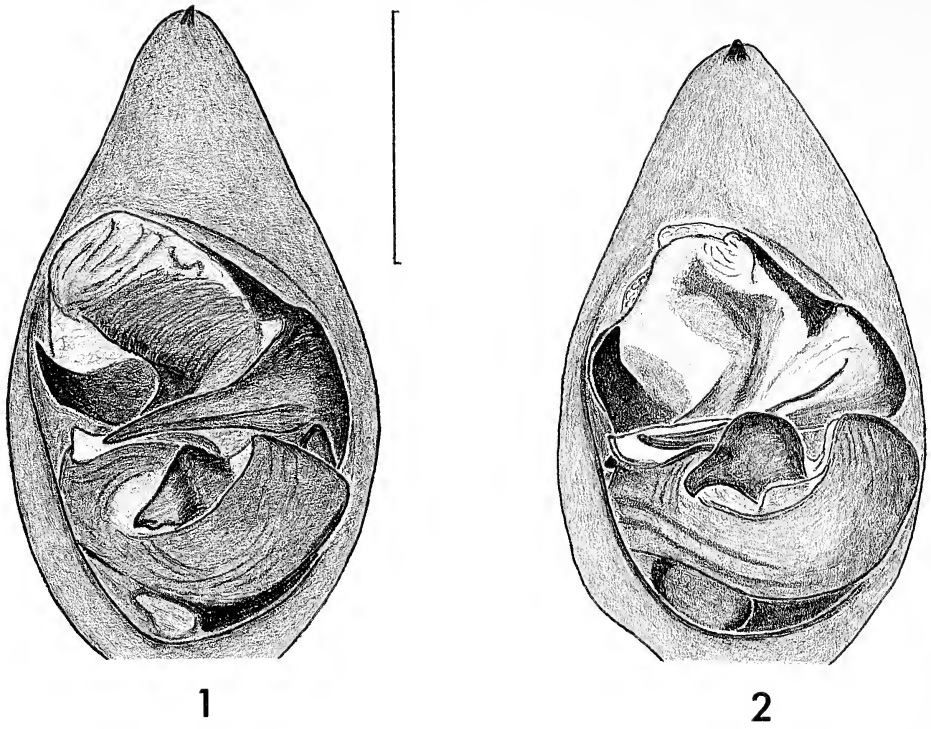
Pardosa wasatchensis Gertsch, 1933: 25, fig. 37 (female holotype from United States: Utah, Sevier County, Fish Lake, in AMNH, examined). Roewer 1954: 195. Bonnet 1958: 3431.

Pardosa subra Chamberlin & Ivie, 1942: 30, fig. 71 (female holotype from United States: Oregon, Harney County, Malheur Lake, in AMNH, examined). Roewer 1954: 194. **Syn. n.**

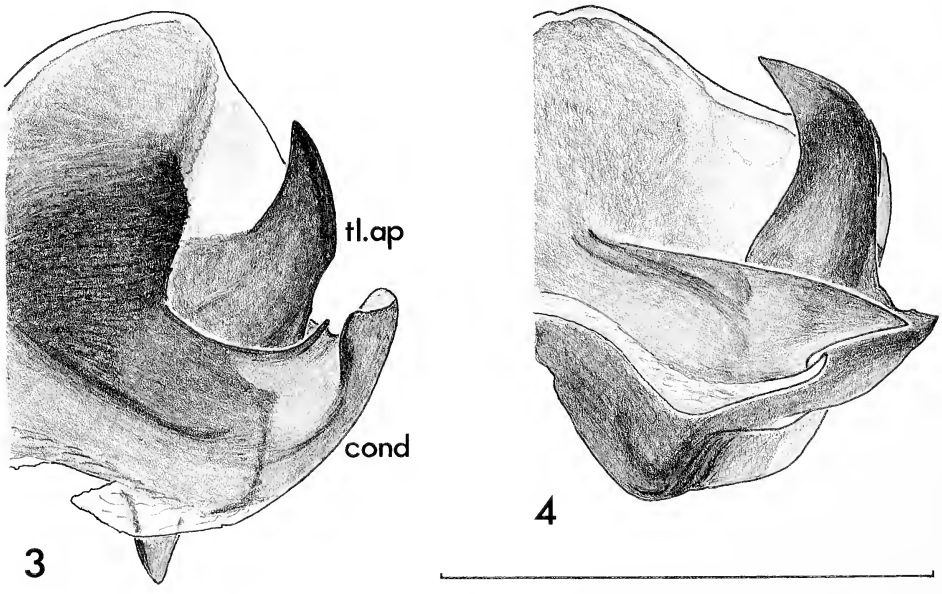
Diagnosis.—Males may be distinguished by the short, only slightly curved embolus, somewhat widened toward its tip, the latter with a small incision on its inner side (Fig. 5), as well as by the configuration of the conductor (Fig. 3) and the retrolateral grooved process of the terminal apophysis (Fig. 10); females by the proportions of the flask-shaped epigyne, with a narrow septum widened posteriorly like an inverted "T", and with anterior transverse pockets well separated and extending more or less laterad (Figs. 14, 15).

Male.—(Utah, Sevier County, Fish Lake). Total length 7.4 mm; carapace 3.60 mm long, 2.65 mm wide.

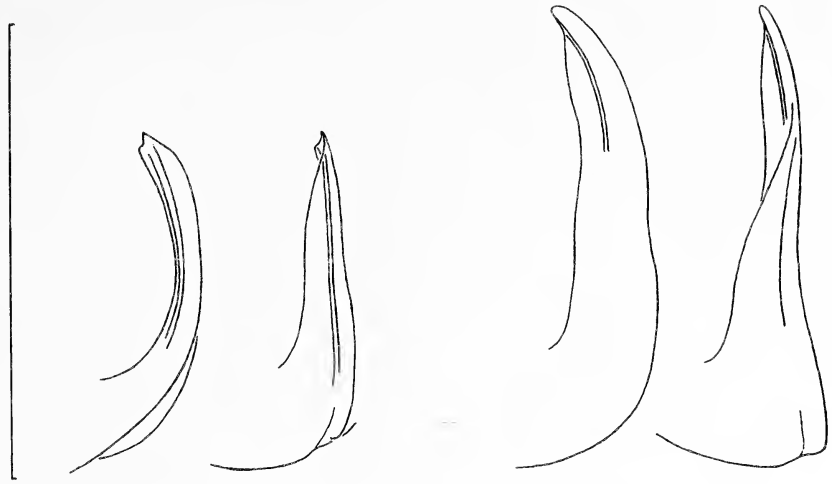
Carapace: Dusky brown, median band in thoracic part yellowish, lateral bands light brownish to yellowish. Lateral bands broken into (2–)3 parts



Figures 1, 2.—Right male palp, ventral view. 1. *Pardosa wasatchensis* Gertsch from Fish Lake, Utah; 2. ***P. vogelae*** sp. n. from Leidy Peak, Utah. Scale: 0.5 mm.



Figures 3, 4.—Terminal part of left palp with conductor (*cond*) and terminal apophysis (*tl.ap*). 3. *Pardosa wasatchensis* Gertsch from 8 mi. N Fish Lake, Utah; 4. ***P. vogelae*** sp. n. from Leidy Peak, Utah. Scale: 0.5 mm.



Figures 5–8.—Embolus seen in frontal (5, 7) and ventral (6, 8) views. 5–6. *Pardosa wasatchensis* Gertsch from 8 mi. N Fish Lake, Utah; 7–8. ***P. vogelae*** sp. n. from Leidy Peak, Utah. Scale: 0.5 mm.

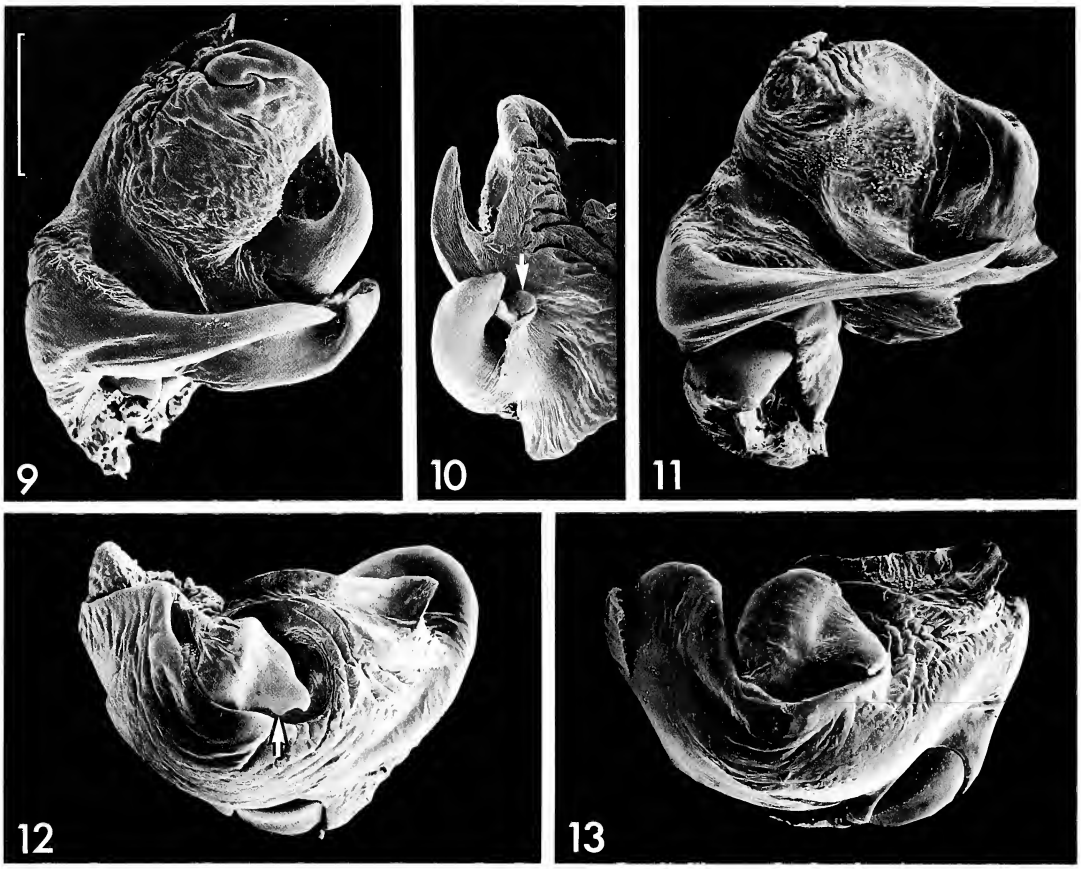
Table 1.—Leg I–IV measurements (mm) of *Pardosa wasatchensis* Gertsch and ***Pardosa vogelae*** sp. n. Fe = femur, Pa = patella, Ti = tibia, Mt = metatarsus, Ta = tarsus.

	Fe	Pt	Ti	Mt	Ta	Total
Pardosa wasatchensis						
Male						
I	2.80	1.30	2.35	2.40	1.65	10.50
II	2.70	1.25	2.15	2.40	1.60	10.10
III	2.65	1.20	2.10	2.80	1.55	10.30
IV	3.40	1.40	2.90	4.20	2.00	13.90
Female						
I	2.70	1.30	2.05	2.05	1.45	9.55
II	2.65	1.30	1.90	2.10	1.45	9.40
III	2.55	1.20	1.90	2.55	1.40	9.60
IV	3.50	1.40	2.90	4.35	2.00	14.15
Pardosa vogelae						
Male						
I	2.30	1.10	1.85	2.10	1.55	8.90
II	2.30	1.10	1.75	2.05	1.50	8.70
III	2.25	1.00	1.70	2.45	1.45	8.85
IV	2.95	1.20	2.40	3.70	1.90	12.15
Female						
I	2.25	1.10	1.75	1.75	1.30	8.15
II	2.25	1.05	1.60	1.75	1.30	7.95
III	2.20	1.00	1.65	2.15	1.25	8.25
IV	2.95	1.20	2.45	3.55	1.75	11.90

by transverse brownish streaks. Postocular spots in cephalic part brownish. Sides of thoracic part with numerous short dark and recumbent grayish hairs. Median band with whitish hairs, in preserved specimens usually remaining behind fovea; around fovea in addition with short dark (and at midline with few long dark) erect hairs. Lateral bands with dark and light hairs. Clypeus yellowish, with long forwardly directed dark hairs medially. Chelicerae yellowish to brownish with grayish brown streaks, furnished with dark hairs. Sternum dark brown, furnished with erect dark and recumbent grayish hairs.

Eyes: Width of row I 52 (slightly procurved as seen from front), row II 71, row III 94, row II–III 70. Diameter of AME 12, ALE 10, PME 26, PLE 21. Distance between AME 8, between AME and ALE 2.

Abdomen: Dorsally grayish brown, with light brownish to yellowish, dark-bordered lanceolate stripe in front. Posteriorly on each side of median part a dark irregular line interrupted at intervals by light dots (with white hair tufts). Median part with two separate spots at end of lanceolate stripe, rearwards followed by two close spots and more posteriorly by a few bars, all brownish to yellowish (pattern sometimes hardly discernible), each spot with one dark dot, bars with two dark dots, each carrying long dark hair. Dorsum and sides with long erect and short dark as well as recumbent light hairs, venter brownish to yellowish with recumbent white pubescence and numerous



Figures 9–13.—Terminal part (9, 11 in ventral view; 10 in retrolateral view) and tegulum with tegular apophysis (12, 13 in ventral view), left male palp (for *arrows* see text). 9–10, 12. *Pardosa wasatchensis* Gertsch from 8 mi. N Fish Lake, Utah; 11, 13. ***P. vogelae*** sp. n. from Leidy Peak, Utah. Scale: 200μm.

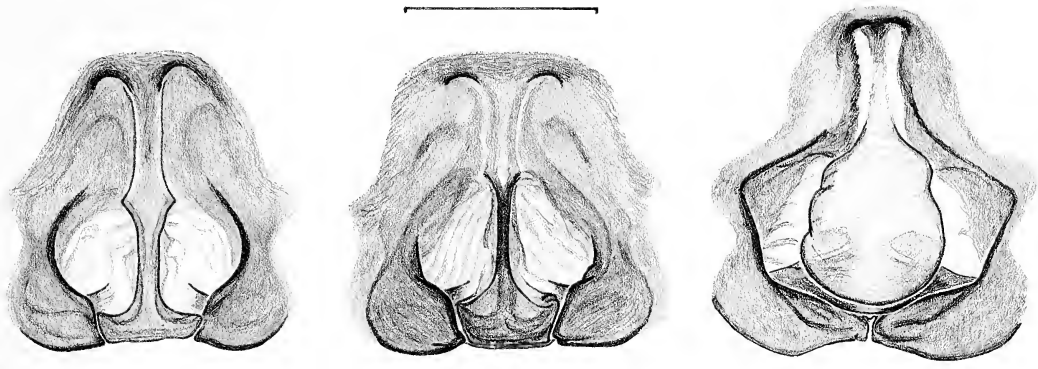
longer erect grayish to light hairs (latter seen only in some males examined).

Legs: (Table 1) Yellowish. Femora with darker blotches dorsally ("pseudoannulation"), outer segments with very faint grayish tinge, on tibiae and metatarsi arranged like the more distinct annulation in female. Tibia I with two or only distal retrolateral spine(s) present. Hairiness of leg I as in rest of legs.

Palp: Patella 0.70 mm, tibia 0.65 mm, cymbium 1.35 mm. Femur, patella and tibia yellowish; femur with dark markings, patella and tibia less so, sometimes even unicolorous. Cymbium brown to blackish brown, lighter apically. Femur, patella and tibia with dark and whitish hairs, latter dominating on tibia; cymbium with dark hairs except distally. Tegulum comparatively protruding. Tegular apophysis as seen in ventral view (Figs. 1, 12) with subtriangular basal part (including anteriorly directed branch); lateral process basally almost as wide as length of basal part and tapering toward ventrally directed slightly hook-shaped tip; posterior (lower in figures) rim of lateral process with more or less distinct denticle-like projection at some distance from tip (*arrow* in Fig. 12). Terminal apophysis (as seen in ventral view: Figs. 3, 9) with heavily sclerotized tooth-like process protruding forward, and with small, grooved retrolateral process (*arrow* in Fig. 10; hidden below conductor in ventral view). Conductor with distal part curved dorsad (Fig. 10); its posterior rim folded towards rounded tip, forming groove (Figs. 3, 9); anterior rim more or less incised before rounded tip. Embolus (Figs. 5, 6) short, in frontal view slightly widening distally, incised at tip.

Female.—(Utah, Sevier County, Fish Lake). Total length 6.7 mm (carried egg sac); carapace 3.70 mm long, 2.70 mm wide.

Similar to male in color pattern and hairiness.



Figures 14–16.—Epigyne, ventral view. 14. *Pardosa wasatchensis* Gertsch, holotype; 15. holotype of *P. subra* Chamberlin & Ivie; 16. ***P. vogelae*** sp. n. from Leidy Peak, Utah. Scale: 0.5 mm.

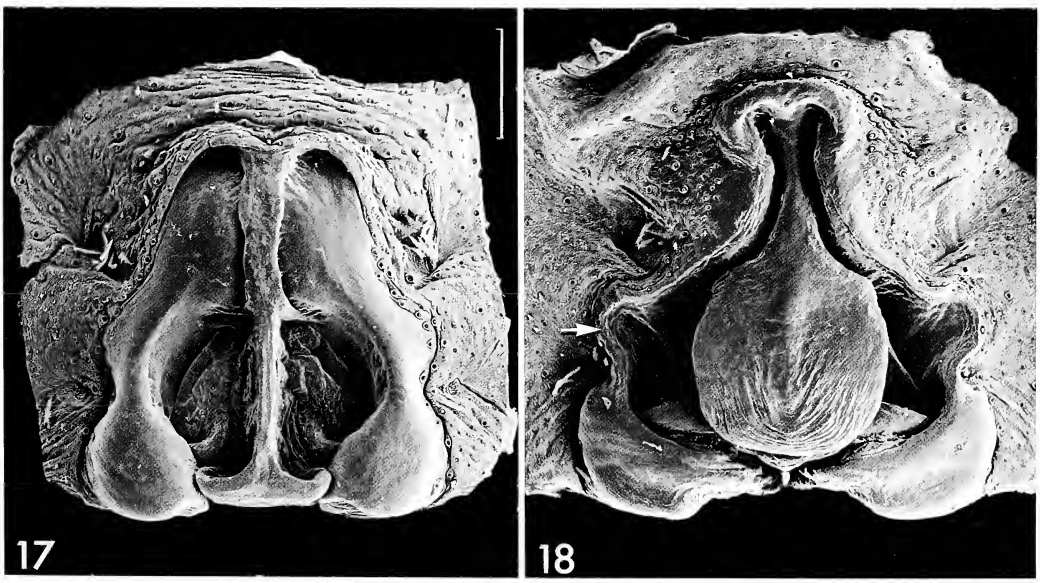
Carapace lighter brownish than in male, and with yellowish, sometimes unbroken, lateral bands with more light hairs. Chelicerae usually lighter than in male and furnished with light hairs in addition to dark ones.

Legs: (Table 1) Femora yellowish to light brownish with darker brownish "pseudoannulation," tibiae and metatarsi brownish, often with very indistinct lighter brown to yellowish annulation. Tibia I with two, only distal, or no retrolateral spine(s) present.

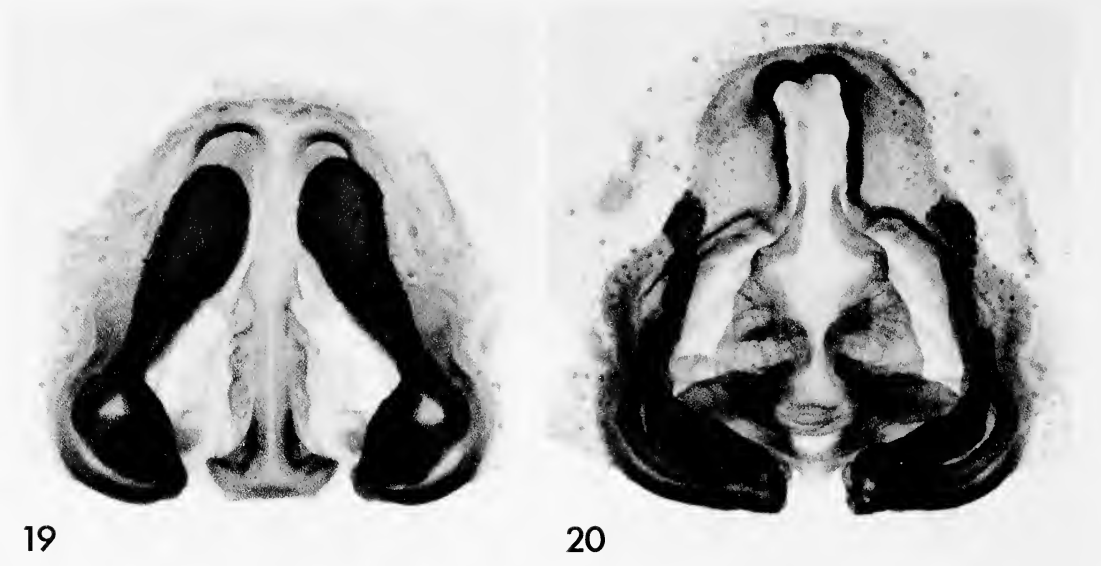
Epigyne: Flask-shaped (Figs. 14, 15, 17; cleared Fig. 19). Anterior transverse pockets well separated, extending laterad. Septal ridge as wide as or slightly wider than narrow septum. Septum posteriorly widened. Lateral elevations sometimes sloping smoothly into anterior part of cavities (i. e., without distinct rim). Receptacles comparatively inflated (Fig. 19).

One female (carapace length 3.40 mm) carried an egg sac with diameter of 4.7 mm and height of 3.7 mm, containing 67 pulli (larvae).

Size variation.—Carapace lengths of material measured: males 3.00–3.60 mm ($n = 15$), females 2.75–3.70 mm ($n = 15$); tibia I length *vs.* carapace length in Fig. 21a.



Figures 17, 18.—Epigyne. 17. *Pardosa wasatchensis* Gertsch from 8 mi. N Fish Lake, Utah; 18. ***P. vogelae*** sp. n. from Leidy Peak, Utah (for *arrow* see text). Scale: 200μm.



Figures 19, 20.—Epigyne (cleared), ventral view. 19. *Pardosa wasatchensis* Gertsch from 8 mi. N Fish Lake, Utah; 20. ***P. vogelae*** sp. n. from Leidy Peak, Utah.

Material examined.—UNITED STATES. *Colorado.* Eagle County: 2 mi. S Burns, 27 June 1963 (B. Vogel, AMNH), 1♂ 2♀. Grand County: S Granby, 26 June 1940 (W. Ivie, AMNH), 2♂ 3♀; 5 mi. S Parshall, 20 June 1963 (B. Vogel, AMNH), 1♂. *Idaho.* Bear Lake County: Nounan, 9 August 1931 (W. J. Gertsch, AMNH), 1♀. Payette County: Payette, 1956 (Evadina Ivie, AMNH), 3♂ 1♀. Teton County: Victor, 15 August 1940 (W. Ivie, AMNH), 2♀. Valley County: Cascade, 5 July 1943 (W. Ivie, CNC), 2♂ 2♀; S Donnelly, 5 July 1943 (W. Ivie, AMNH), 1♀. *Montana.* Horse Prairie (not located), 11 July 1935 (W. Ivie, AMNH), 2♀. Jefferson County: S Butte, Toll Mt. Campground, 6 August 1964 (D. C. Lowrie, AMNH), 1♀. *Oregon.* Harney County: Malheur Lake, 18 June 1940 (L. W. Saylor, AMNH), 1♀ (holotype of *P. subra*). *Utah.* Rich County: Bear Lake (S end), 26 June 1962 (W. Ivie, AMNH), 1♀. Salt Lake County: Salt Lake City, September 1930 (W. J. Gertsch, AMNH), 1♀. Sevier County: Fish Lake, 4 September 1929 (Chamberlin & Gertsch, AMNH), 1♀, 22–23 June 1930 (W. J. Gertsch, AMNH), 3♀ (incl. holotype), 13 July 1931 (W. J. Gertsch, AMNH), 1♂, 1 July 1940 (Gertsch & Hook, AMNH), 2♂ 4♀; Sevenmile Creek 8 mi. N Fish Lake, 9400 ft, 14 July 1973 (B. R. Vogel, BRV, NRS), 3♂ 18♀. Summit County: W Wasatch Station, 3 June 1933 (W. Ivie, AMNH), 1♂ 1♀. *Washington.* Douglas County: 5–10 mi. E Bridgeport, prairie community, in wet area, amongst *Artemisia*, 7 July 1964 (D. C. Lowrie, AMNH), 1♀. *Wyoming.* Teton County: Grand Teton National Park, S Jackson, 24 June 1938 (W. Ivie, AMNH), 1♂; Grand Teton National Park, Moran area (Jackson Hole Biological Research Station, Uhl Hill &c.), July–August 1961–69 (D. C. Lowrie, AMNH), 2♂ 17♀; Grand Teton National Park, Lake Solitude, moist meadow, 3 August 1962 (D. C. Lowrie, NRS), 1♂; Teton National Forest (all near Gros Ventre R.), Bridge Creek, in moist sedge-grass field, 30 August 1964 (D. C. Lowrie, CNC), 3♀; same, Lafferty Creek, in moist willows, 30 August 1964 (D. C. Lowrie, NRS), 1♀; same, nr Soda Lake, 30 August 1964 (D. C. Lowrie, AMNH), 5♀. Uinta County: 10 mi. E Evanston, 18 July 1935 (W. Ivie, AMNH), 1♀; Yellowstone National Park: Bridge Bay, 9 July 1935 (W. Ivie, AMNH) 1♂ 2♀, 20 June 1938 (W. Ivie, AMNH), 21♂ 16♀; Yellowstone Lake, 21 June 1938 (W. Ivie, AMNH), 1♀.

One ♂ from Canada, Ontario, St. Thomas, 1928 (McBride, AMNH) is believed to be incorrectly recorded (cf. Dondale & Redner 1986:818 concerning material of other *Pardosa* species incorrectly recorded from St. Thomas).

Habitat.—According to Lowrie (1973:110) "a moist meadow form. . .[but] further characterization of its microhabitat is needed."

Pardosa vogelae, new species
Figs. 2, 4, 7, 8, 11, 13, 16, 18, 20, 21b, 22; Table 1

Type.—Male holotype from United States: Utah, Daggett County, Leidy Peak, 11,500 ft (Beatrice R. Vogel & C. Durden), deposited in AMNH.

Etymology.—Named for Dr. Beatrice R. Vogel, one of the collectors, who has contributed substantially to the exploration of the North American lycosid fauna.

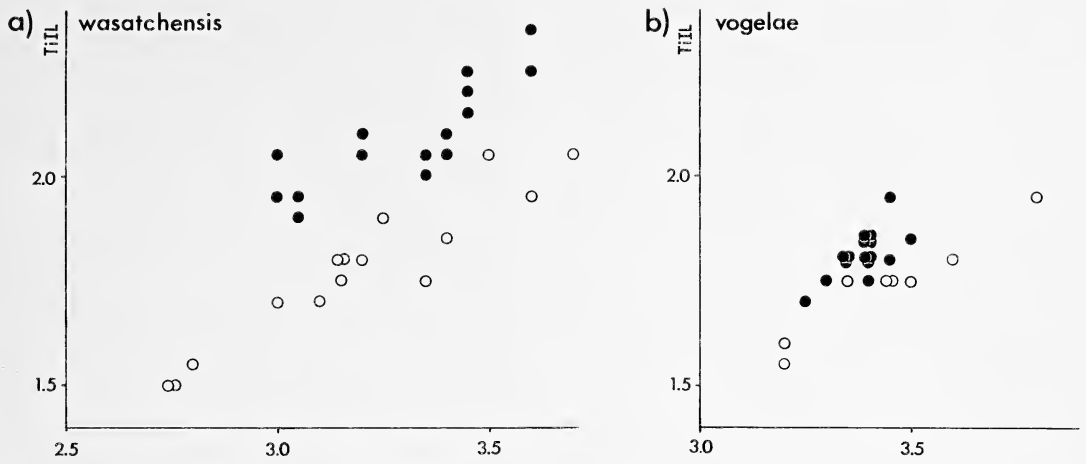


Figure 21.—Tibia I length (TiIL)/carapace length in adult males (closed circles) and females (open circles). a) *Pardosa wasatchensis* Gertsch; b) ***P. vogelae*** sp. n.

Diagnosis.—Males may be distinguished by the very prominent, curved and pointed tooth of the terminal apophysis, and by the configuration of the conductor (Fig. 4); females by the proportions of the flask-shaped epigyne, with a very wide septum and the rims of lateral elevations characteristically curved (Fig. 16).

Male.—*Holotype:* Total length 6.6 mm; carapace 3.40 mm long, 2.45 mm wide.

Carapace: Dusky brownish; median band in thoracic part yellowish; lateral bands light brownish, uneven in width and with darker breaks, not continuous to clypeus. Postocular spots in cephalic part brownish. Sides of thoracic part with numerous short dark hairs, fewer recumbent grayish ones, and some longer erect, somewhat wavy hairs. Median band with recumbent whitish hairs, around fovea additionally with short and few long erect dark hairs. Clypeus yellowish, in apparently old specimens now available devoid of hairs except long forwardly directed dark ones. Chelicerae brownish with darker streaks, distally yellowish on inner side, furnished with dark hairs. Sternum blackish brown with small light median stripe in front, furnished with recumbent light and more erect dark hairs.

Eyes: Width of row I 48 (slightly procurved as seen from front), row II 65, row III 85, row II–III 62. Diameter of AME 10, ALE 10, PME 24, PLE 19. Distance between AME 7, between AME and ALE 2.

Abdomen: Dorsally grayish brown; posteriorly on each side of median area a row of darker patches with light dots between patches. Light grayish brown, dark-bordered lanceolate stripe in front. Dorsum with long erect and short dark hairs as well as light hairs (latter numerous in lanceolate stripe). Sides of abdomen mottled with yellowish brown spots on grayish background. Venter brownish with recumbent white pubescence and scattered erect dark hairs.

Legs: (Table 1) Femora yellowish with sooty brown dorsal markings, less sooty ventrally. Outer segments yellowish to light brownish. Hairiness of leg I as in rest of legs. Tibia I with two, only distal or no retrolateral spine(s).

Palp: Patella 0.65 mm, tibia 0.65 mm, cymbium 1.35 mm. Femur, patella, tibia and cymbium dusky brownish; femur with darker markings, cymbium lighter distally. Patella with dark hairs, tibia with numerous long and short dark hairs, cymbium with dark hairs except distally. Tegular apophysis in ventral view (Figs. 2, 13) shaped like bird's head, with bulky, rounded basal part (including anteriorly directed branch); lateral process shorter than width of basal part, not considerably narrowing before slightly hook-shaped tip. Terminal apophysis (in ventral view: Figs. 4, 11) with curved, heavily sclerotized tooth-like process protruding forwards, tip acute; sclerotized retrolateral process, end pointed; heavily sclerotized rounded portion protruding posteriad. Conductor (as seen in Figs. 4, 11) distally bifurcate, upper branch longest, evenly tapering to pointed tip; lower branch short, unsclerotized. Embolus as in Figs. 7, 8.

Female.—*Allotype:* Total length 6.5 mm (carried egg sac); carapace 3.35 mm long, 2.45 mm wide.

Similar to male in color pattern and hairiness.

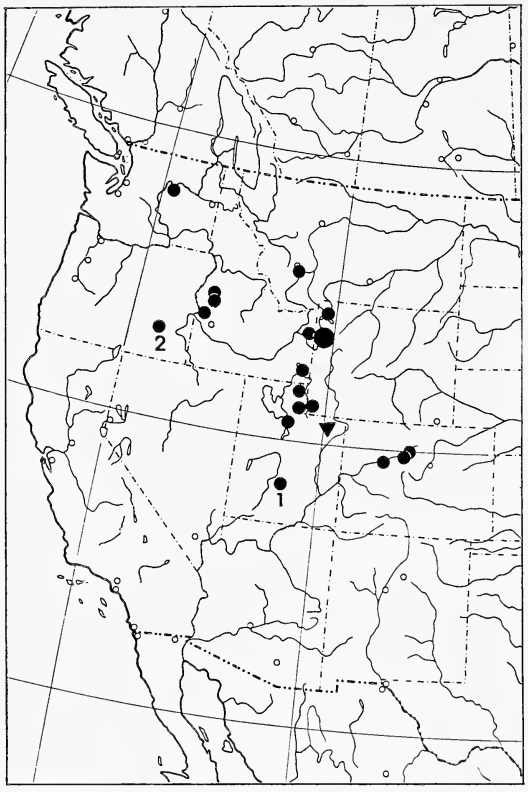


Figure 22.—Collection localities of *Pardosa wasatchensis* Gertsch (circles) and ***P. vogelae*** sp. n. (triangle). Type localities of *P. wasatchensis* (1) and *P. subra* Chamberlin & Ivie (2). Large circle refers to more than three close localities.

Carapace with more distinct yellowish median and broken lateral bands, latter with whitish hairs. Lanceolate stripe on abdomen more clear yellowish.

Legs: (Table 1) Brownish; femora laterally yellowish, at least in distal half, sometimes with traces of darker pseudoannulation; tibia I with no or only distal retrolateral spine.

Epigyne: Flask-shaped (Figs. 16, 18; cleared Fig. 20). Narrow indistinct (unsclerotized) septal ridge continuing into very wide septum, evenly rounded posteriorly. Sclerotized rim of lateral elevations characteristically curved (Fig. 18, *arrow*). Lateral elevations coming close posteriorly, separated by narrow slit. Two deep pockets covered by septum in front of extensive cavity sclerites. Receptacles comparatively narrow (Fig. 20).

Size variation.—Carapace lengths of material measured: males 3.25–3.50 mm ($n = 16$), females 3.20–3.80 mm ($n = 8$); tibia I length *vs.* carapace length in Fig. 21b.

Material examined.—UNITED STATES. *Utah.* Daggett County: Uintah Mountains, Spirit Lake, August 1935 (D. Cottam, AMNH), 1♀. Daggett & Uintah Counties: Leidy Peak, 11,500 ft, 5–6 August 1964 (B. R. Vogel & C. Durden, AMNH, BRV, CNC, MCZ, NRS), 16♂ 7♀ (incl. holo- and allotype from 5 August).

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NEWLY-DISCOVERED SOCIALITY IN THE NEOTROPICAL SPIDER *AEBUTINA BINOTATA* SIMON (DICTYNIDAE?)

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ABSTRACT. The neotropical spider *Aebutina binotata* Simon (Dictynidae?), previously known from a few museum specimens, was discovered to live in colonies and to exhibit highly cooperative behaviors that would classify it as non-territorial, permanently social. Colonies of this species, that contained from 14–106 adult females plus their offspring, were observed in a tropical rainforest site in Eastern Ecuador. The spiders occupied communal nests in which they cooperated in prey capture and fed communally on the prey. Large prey items were moved to the feeding site by the coordinated effort of two or three individuals. The spiders periodically carried out web maintenance activities; but when widespread damage to the nest occurred, they moved as a group to a new location. Care of the brood appeared to be communal since the offspring from different mothers intermixed in the colonies and were all cared for by a decreasing number of surviving females. Adult females participated most heavily in all the activities of the colonies, with no apparent division of labor among them. In particular, no reproductive division of labor was observed: all adult females in colonies observed throughout the egg-laying period apparently laid a single egg sac each.

The most advanced form of social behavior known for spiders involves cooperation among members of a colony in building and maintaining a communal nest, capturing prey on which to feed communally, and taking care of the offspring (Buskirk 1981; D'Andrea 1987). These tasks are performed by members of the same generation without any apparent division of labor among them (Darchen & Delange-Darchen 1986). In particular, unlike what occurs in the most highly social insects (Wilson 1971), no specialized reproductive castes are present in social spiders: most, if not all (Vollrath 1986), individuals in a social spider colony apparently bear offspring. This form of social behavior, labeled as non-territorial permanently social (D'Andrea 1987) or quasisocial (Wilson 1971), has arisen independently in at least six spider families. To date, a total of 14 species in eight genera have been described as possessing the traits that would define them as having attained this level of sociality (for partial lists see Buskirk 1981; and D'Andrea 1987; for species not included in these partial lists, see Main 1988, Rypstra & Tirey 1989; Avilés in press 1, in press 2). Ten of these species have been described or their sociality discovered in the last 30 years, indicating that highly cooperative behavior in spiders, although rare relative to the total number of spider species (about 40,000 described species), is perhaps more widespread than previously believed.

Here, I report on newly discovered sociality in the neotropical cribellate spider *Aebutina binotata* Simon (Simon 1892). This species was described by Simon at the end of the last century from a few female specimens collected in the Brazilian Amazonas Province (Simon 1892). From a systematic point of view, *Aebutina binotata* has proven to be an enigmatic species whose placement in any of the currently described spider families is not fully resolved (Lehtinen 1967). The genus *Aebutina*, of which *A. binotata* is the type species, is temporarily assigned to the Dictynidae (Petrunkevitch 1928; Millot 1933), after having been originally placed by Simon (1892) in the Uloboridae. Previous to the present study, no information on the life history or behavior of *A. binotata* was available. The observations that I report here indicate that this species is colonial and that it exhibits the strongly cooperative behaviors common to non-territorial permanently social spiders.

In this paper I describe the structure of the nests and colonies and report on behavioral aspects of the sociality of this species: observations involving cooperation on web maintenance and repair, colony relocation, prey capture and transport, food sharing, communal brood care, and

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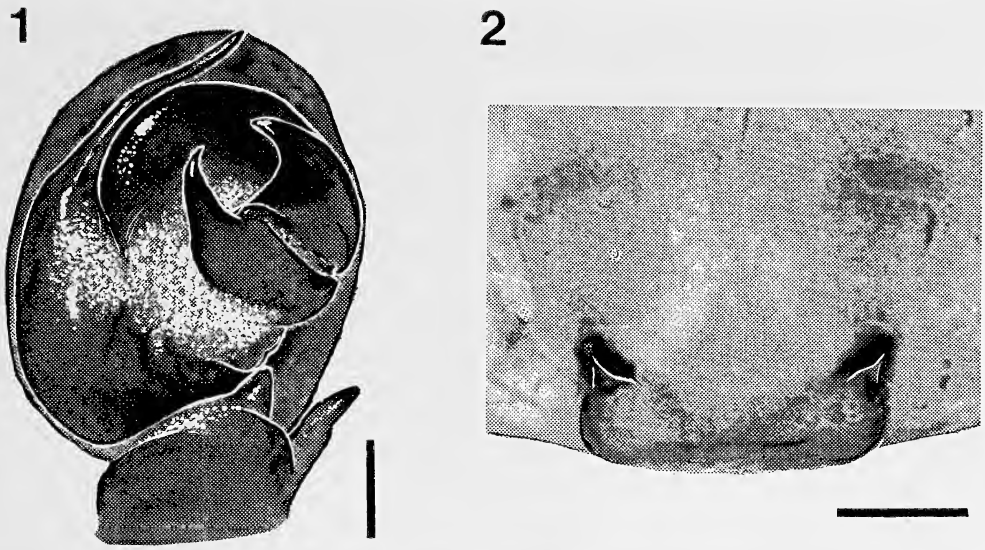


Figures 1, 2.—*Aebutina binotata* genitalia: 1. Male; 2. Female. Drawings from computer digitized images by W. Maddison. Scale bars correspond to 0.1 mm.

tolerance to members of other colonies. Even though not directly related to sociality, I also present observations on courtship and mating.

METHODS

The spider.—Live adult females of *A. binotata*, which measure about 5 mm in length ($\bar{x}$ = 4.7, n = 7), have a diamond-shaped, bright yellow abdomen with a black spot on each side (therefrom the name *binotata*). The males (3.4 mm when adult, n = 2) and early-instar individuals are also yellow, of less intense coloration and with somewhat less clearly marked spots. Males are adult in the 7th instar while females are adult in the 8th instar (Avilés 1992). The egg sacs are spherical and measure around 3.5 mm in diameter. They consist of a mesh of white silk that surrounds the yellow-colored embryos.

One of the reasons for the uncertainty in the systematic placement of *A. binotata* has been the lack of male specimens (Lehtinen 1967). In connection with the present study I collected males which have been deposited in the collections of the Museum of Comparative Zoology, Harvard University. In this study I do not address the systematic placement of *A. binotata*. However, I provide drawings of male and female genitalia for future reference (Figs. 1, 2). Initial determination of the female specimens was done by J. Hunter of the MCZ and later confirmed by comparison with the types by H. W. Levi.

The observations.—I studied colonies of *A. binotata* in a tropical rainforest site by the Tarapuy River in Eastern Ecuador, Sucumbios (formerly Napo) Province (0° 08′ S, 76° 16′ W, 210 m above sea level). I first discovered two colonies in January 1983 and then an additional one in February 1984. From this date to September 1984, I visited the area on six occasions and identified a total of 44 colonies (24 up to a July visit and 20, either new or previously recorded colonies that had relocated themselves, in the September visit).

For each colony observed, I recorded its position, distance from the ground, and structure of the nest, including the size of the leaf (or leaves) supporting the colony and the percent of the leaf (or leaves) occupied. I counted the total number of adult females, egg sacs, and males present in the colonies, and estimated the number of juveniles of different size classes (i.e., instars).

I conducted behavioral observations on an opportunistic basis. Observations were conducted during the day, usually between 900 and 1800 h, on one occasion from 700 h. Activities involving nest maintenance and repair were observed regularly in the colonies. I observed one complete short-distance colony relocation event, a portion of another, and a 13-hour period (1200–1800 h and 700–1400 h of the day after) of one long-distance relocation event. I also obtained indirect evidence of six other relocation events. I recorded complete sequences of prey capture, including prey transportation and initiation of

feeding, on 13 occasions, and on five others after feeding had been initiated. Four cases of prey rejection were observed. Other prey capture or feeding events were observed on a more casual basis. I observed courtship and mating for a period of 100 min (1215–1400, August 4, 1984) in one colony containing four adult males and 106 females. I observed a total of four copulations and 16 unsuccessful mounting attempts. One additional copulation was observed at an earlier date in a different colony (colony 5, May 20, 1155 h). A pilot test of tolerance to conspecifics involved the introduction of one adult female into a foreign nest. Additionally, for ten weeks I maintained in the laboratory two colonies on which I conducted casual behavioral observations.

RESULTS

The nest and colonies.—The nests of *A. binotata* are basically two-dimensional structures consisting of one or a few contiguous leaves and their connecting branches covered on both surfaces by a continuous layer of silk (Fig. 3). The outer surface of the web is covered by cribellate silk that cause insects to get entangled when landing on it. The sheet of silk on the underside of the leaves (the lower web) is not attached to the leaf blade, but separated by an open space that is used by the spiders as refuge. Egg sacs and spiderlings occupy this space, sitting on the inner surface of this lower web and congregated towards the center. Openings allow spiders to move freely from one surface of the web to the other. Adult spiders sit on the outer surface of the lower web, lined up along the edges of the leaf (Fig. 4) in a position that allows them rapid access to the top of the leaf where insects usually get entangled. Major perturbations to the nest, such as experimental shaking, cause the larger individuals in a colony to drop to the ground on silk draglines along which they return once the disturbance has stopped.

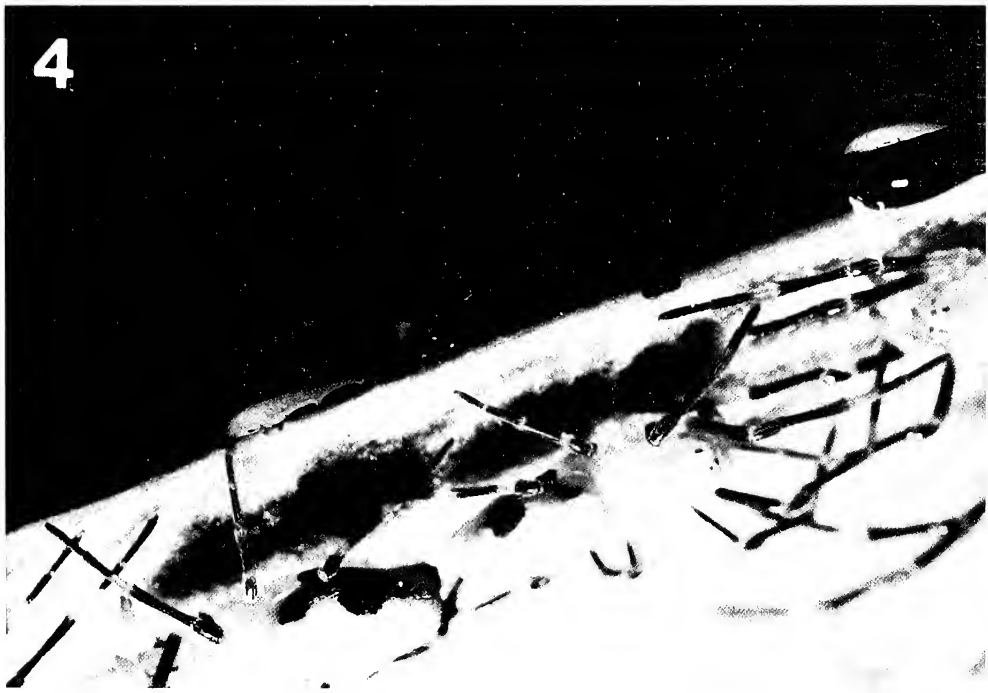
The size of the colonies, measured as the number of adult females present in a colony around the time the eggs were being laid, ranged from 14–106 (n = 19, median = 40, mean = 46.7 ± 11.8, 95% conf. int., Fig. 5). Colonies with young spiderlings could contain up to eight hundred individuals; but, because of the smaller size of the young, the total biomass was probably within a similar range. The area occupied by a nest was found to be proportional to the number of adult females present (Fig. 6); it ranged from 74–200 cm^2 and included either a portion of a large leaf or several small leaves. Nests were found between 0.5 m and 4.5 m from the ground, although nests occurring higher than this would have probably been missed. The nests appeared invisible when seen from above and could only be located by looking for the spiders underneath leaves. From below, the appearance of the colonies was striking because of the bright yellow coloration of the adult females and spiderlings and the whiteness of the egg sacs.

Web construction and repair.—The nests were constructed and maintained cooperatively. Web maintenance activities involved: (a) periodically adding cribellate silk to maintain the stickiness of the web, (b) removing and replacing damaged web following destruction by the rain, (c) repairing holes left by ensnared prey, and (d) throwing out debris. All these activities could be simultaneously performed by several individuals in different areas of the nest. For instance, in a nest of 13 adults and around 190 juveniles, web repair after a rain storm required about two hours during which 16–26 spiders working at a time removed the damaged silk, added new silk lines across the surface of the leaves, and added a final layer of cribellate silk.

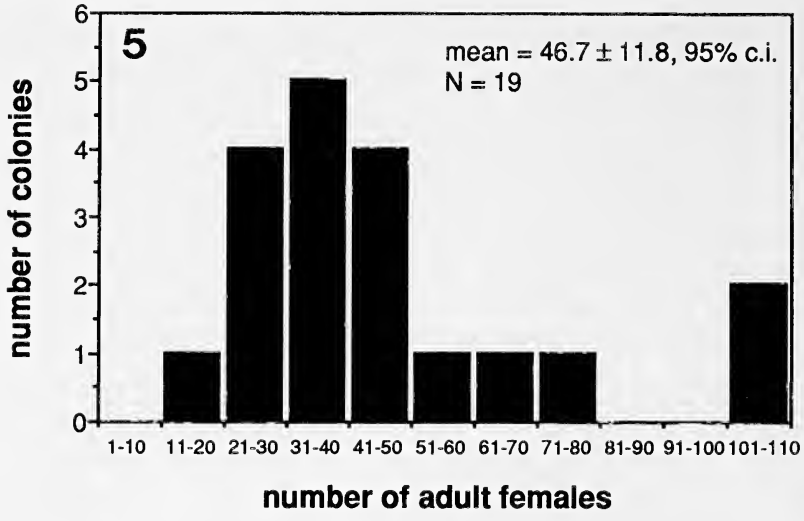
Unlike other social spiders where regular web reinforcement activities take place exclusively at sunset (e. g., in *Anelosimus eximius*, Tapia & De Vries 1980), *A. binotata* spiders added cribellate silk periodically throughout the day. The spiders were inactive in colonies seen early in the morning (around 700–730 h) and all activity seemed to have ceased in two colonies observed at 1800 h. At this time the spiders retreated to the underside of the leaves and presumably carried out only prey capture activities until the following day.

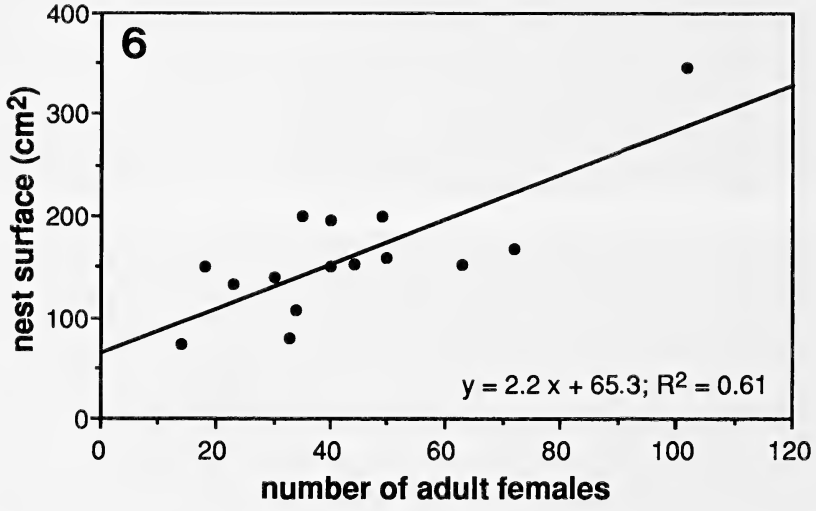
Colony relocation.—Extensive destruction of the web resulted in colonies abandoning their original nest. One of the colonies, for instance, moved to a leaf 12 cm from its original location after the leaf that supported its nest dried out. At later dates, this and three other colonies moved from 0.3–4.5 m after a heavy rain destroyed their nests. Colony relocation involving much greater distances (>> 5 m), independent of web destruction, apparently took place prior to mating and egg laying (Avilés 1992).

Just prior to colony relocation, a fraction of the spiders in a colony could be seen initiating the production of airborne silk lines by hanging down 2–5 cm from their nest (see Eberhard 1987



Figures 3, 4.—*Aebutina binotata* colonies in Tarapuy, Ecuador: 3. Whole nest; 4. Adult females lined up along the edge of their nest.





Figures 5, 6.—5. Number of adult females (and/or egg sacs, whichever is larger) present in *Aebutina binotata* colonies seen sometime immediately before or during the egg laying period; 6. Correlation between the number of adult females in a colony and the surface occupied by their nest (measured in cm^2).

for method of airborne line production). Once a dragline became attached to the nearby vegetation it was first followed by the spider that originated it and then by other spiders. Even if there were draglines attaching in different directions, all spiders eventually moved along a single dragline since the spiders following an isolated route returned to join the majority. This method was repeated from one stop to the next until the eventual settlement of the colony. In the cases observed, all individuals in a nest moved to the new location.

The relocation of a colony could be completed in a few hours or in consecutive days. For instance, a colony with eight adult females and more than 200 juveniles (mostly 4th-instar) moved to a location 30 cm away in the span of 5–6 hours. Another colony that contained eight adult females and approximately 350 3rd–5th instar juveniles moved first to an intermediate stop 1.8 m from its original location, remained there for a period of a day and then continued on for an additional meter. Colonies migrating previous to mating and egg laying appear to migrate for longer periods. For instance, a colony with adult males and females that I followed for

13 hours had not settled when I stopped the observations after a day and a half and 50 m of group migration (Avilés 1992).

Prey capture and feeding.—Prey capture involved the simultaneous participation of 1–6 individuals, apparently depending on the size of the prey and the efforts it made to free itself. If present in sufficient numbers, only the adult females participated in prey capture, though later-instar spiderlings would participate when there were relatively few adult females in the nest or the prey were small. The females placed along the edge of the nest closest to an struggling insect would rush towards it and attack it by first biting its appendages and then other parts of the body. Once completely overcome, prey items were moved to the underside of the leaves where feeding took place. Adult spiders initiated prey digestion (Fig. 7) and later left the prey to the juveniles. Prey trapped and consumed included wasps, mosquitoes, cockroaches, one large ant, some beetles. A small coccinelid and another small beetle were rejected. Very large insects, such as a 4 cm long moth and a 2 cm cetonine beetle, were ignored.

Group transport.—Transportation of items around the nest, either prey to be consumed or debris to be thrown out, were also among the activities regularly carried out by the spiders. Small items were handled by individual spiders. The transportation of large objects, on the other hand, required a group effort that was particularly challenging given the sticky nature of the entire surface of the web. Complete group transport events were observed on three occasions. A large ant moved from the upper to the lower surface of the nest, for instance, involved the participation of three individuals. While one individual cut pieces of web to release the ant, the second one pulled and the third pushed the ant in a given direction. Once released, the ant was transported toward the edge of the nest. One individual lifted the ant from below so as to maintain it at a distance from the surface of the web. As this individual walked towards the edge, the other two individuals, one in front and one in the back, helped by pulling and pushing in the required direction. Once at the edge, the ant was successfully moved to the other side by having one spider hold it from above as it walked towards the edge while the other two supported the item and pulled it from below. It took the spiders four minutes to disentangle and bring the ant to the edge, three more minutes to bring it over the edge and onto the other side of the nest, and another three minutes to move it one cm into its final position where feeding was initiated. Two other group transport events observed required two and three individuals to transport an homopteran and a fly, respectively.

Communal brood care.—While most of the adult females lined up along the edges of the nest ready to participate in prey capture, a number of them mounted guard by the egg sacs and spiderlings. Besides sac guarding, parental care included catching prey for the spiderlings and initiating the enzymatic digestion of the prey. Regurgitation feeding was not observed during the study period, though specific studies would be required to confirm its absence.

Two lines of evidence suggest that parental care is communal: (1) the spiderlings in a nest intermix freely, in a way that it does not seem possible for a mother to discriminate between her own and other mother's offspring; and, (2) the number of adult females present in the colonies drops continuously (most likely due to mortality) during the incubation and emergence periods, while all the egg sacs and offspring present in the colonies continue to be cared for. For instance, half the adult females of one of the colonies observed throughout most of its life cycle were already gone by the time their offspring had only reached their third or fourth instar. All the offspring, however, continued to be cared for by the remaining females whose number continued to decrease until none were left by the time the offspring had reached their sixth instar. This indicates that a large majority of the offspring were raised by females other than their mother.

Division of labor.—Adult females tended to participate disproportionately in all the activities of the colony, though later-instar juveniles participated to varying degrees. Later instar juveniles, for instance, handled small prey or participated in group efforts when the relative number of adults in the nest was low. Juveniles were relatively more active in web maintenance activities, particularly in laying down cribellate silk, though the numbers in which they participated were not representative of the proportion in which they occurred in the colonies. For instance, after a storm had destroyed the upper web of one of the colonies under study, all adult females (a total of eight) and 20% of the juveniles (out of a total of 200) were seen removing the damaged web and laying down new strands of silk. In a different colony, which contained 13 adult females and

Figures 7, 8.—*Aebutina binotata*. 7. Group of adult females feeding on a prey; 8. Mating couple in Tarapuy, Ecuador.

around 190 juveniles, 30–100% of the females were active at different times during a two-hour period following a storm, while only 4–7% of the juveniles were. The youngest juveniles that appeared able to participate in activities such as laying cribellate silk belonged to the 4th-instar. Immature males in the colonies kept in the laboratory were seen laying silk during web reinforcement, while it was not possible to determine whether adult males participate in this or any other activity since they were seen in the colonies for only a short period of time.

There was no evidence of division of labor among spiders of a given age group: a task started by one individual was often completed by another and the same individual could be seen carrying out different tasks. Marking experiments, however, are needed to confirm these observations. Regarding reproductive division of labor, in all the colonies observed throughout the egg laying period the total number of eggs cases present was the same as the number of adult females in the nest (Table 1). Since all the egg sacs in a colony were laid within a short time span (Avilés 1992); and thus it is unlikely that some females may have laid more than one case, it follows that all females in the colonies observed reproduced. Reproductive division of labor, therefore, appears absent in *Aebutina binotata*.

Social interactions and tolerance to conspecifics.—The 14 adults and 74 juveniles kept in the laboratory in a 40 × 30 × 30 cm terrarium remained aggregated throughout a 10-week observation period. When they relocated their nest within the terrarium, all the spiders moved together. Encounters between spiders, which were common during the course of their daily activities, involved touching each other with the legs and pedipalps.

Spiders in the field did not appear to discriminate against members of other colonies. One spider experimentally introduced into a foreign nest was initially approached by other spiders, probably in response to the vibrations produced, but was soon treated as a member of the colony. After its introduction, the spider resumed the activity (adding cribellate silk) it had been performing when removed from its native nest. A month later, the spider was still in the colony, and, aside from the experimental mark, was indistinguishable from other spiders in the nest.

Courtship and mating.—I observed courtship and mating in a colony that contained 106 females, 4 males, and 1 egg sac. During the 100 min of observations, three of the males attempted insistently to mount females. Most of the attempts observed (16 out of 18) were rejected by the females who either moved away or resisted. Two resulted in copulations. Two additional copulations had already been initiated when the observations started. Copulations took place with the male over the back of the female and both facing in opposite directions (fig. 8; position "c" in Foelix 1982, p. 195). In one of the matings observed the female remained motionless all through the mounting. In a second mating observed, the male seemed to exert force over the female. The two complete copulations observed lasted around 4 min. Given the disparity in the numbers of males and females, and the observation that most or all the females in a colony lay eggs (see above), it follows that each male is able to fertilize a large number of females.

Table 1.—Number of females and egg sacs laid in *A. binotata* colonies periodically observed throughout the egg laying period. In addition to the 45 egg sacs shown, colony 14 contained newly eclosed juveniles from around four egg sacs.

	Colony				
	9	22	23	14	25
Adult females	102	44	30	48–49	52
Egg sacs present	102	44	29	45+	54

DISCUSSION

The social behavior here described for *A. binotata* has strong similarities with that of other non-territorial permanently social spiders present in the genera *Achaearanea* (Theridiidae), *Agelena* (Agelenidae), *Anelosimus* (Theridiidae), *Diaea* (Thomisidae), *Mallos* (Dictynidae), *Stegodyphus* (Eresidae), *Tapinillus* (Oxyopidae), and *Theridion* (Theridiidae) (Buskirk 1981; D'Andrea 1987; Avilés pers. obs.). These similarities, which include cooperative web building and maintenance, cooperative prey capture, communal feeding, communal brood care, tolerance to members of other colonies, and a lack of castes, are particularly striking given the phylogenetically diverse set of species in which they have evolved.

One feature common to this diverse set of species, which might be to a large extent responsible for these similarities is an irregular type of web, present in all but the social thomisid (Main 1988; Evans & Main 1993), but absent in other colonial but non-cooperative species such as *Metabus*

gravidus or *Philoponella republicana* (Buskirk 1981; D'Andrea 1987). An irregular web is thought to constitute a preadaptation for cooperative behavior in spiders because it allows communal habitation and the simultaneous involvement of more than one individual in web construction and repair as well as in prey capture (Buskirk 1981). Cooperative web building, because it allows the construction of a relatively large area or volume of entangling web, leads to the capture of relatively large prey items, which, in turn, require the concurrence of several individuals for their subjugation. Large prey items can then be shared by several individuals in a nest, leading to communal feeding, a trait common again to the non-territorial permanently-social species studied (Buskirk 1981; see also Main 1988; Rypstra & Tirey 1989), but absent in the colonial orb weavers. A communal nest also facilitates communal care of the brood because it renders discrimination among spiderlings intermixed in a common space impractical.

A. binotata is typical among the non-territorial permanently social spiders in having an irregular type of web and in having developed cooperative prey capture, communal feeding, and communal brood care. As in these other species (Buskirk 1981), cooperation allows *A. binotata* spiders the capture of prey items larger than those single individuals could handle and facilitates the sharing of prey among a larger proportion of colony members than those participating in their capture. The advantages of cooperation in the care of the brood become specially evident in *A. binotata*, where the survival of orphaned offspring is only possible because surviving females indiscriminately care for all the young in a nest (see also Christenson 1984; D'Andrea 1987).

The ways in which the architecture of the nests of *A. binotata* differs from that of other non-territorial permanently social species may be responsible for some of the features that appear unique to this species. One such feature is the cooperative transport of prey items from the site of their capture to their consumption site, a trait that in this species is developed to a greater extent than in any other social spider. Three aspects of the structure of the nests of *A. binotata* pose a special challenge to prey transport in this species: (1) the sticky nature of the web surface; (2) the relatively small capture area; and, (3) the fact that prey items need to be brought over the edge of the leaf with the consequent danger of accidentally dropping them out of the nest. In other cooperative spiders, webbing usually surrounds the prey in all directions during its transport and the nests are considerably larger than the prey being transported, so that their overall efficiency is not critically affected by damage to a portion of the web caused by dragging a prey item.

The instances of group transport that I observed in *A. binotata* required a degree of coordination among the individuals involved that can only be explained if some sort of communication was taking place among them. Prey transport in other species usually involves a number of individuals pulling in the same general direction or some form of, apparently uncoordinated, relay activity (e.g., Ward & Enders 1985). In the genus *Agelena* the prey is either carried by a single individual (Krafft 1971) or eaten on the site of its capture when it is too large for individual transport (Darchen 1967; Krafft 1971). In *Achaearanea disparata* (Darchen 1967) some individuals pull while others aid in cutting the threads that hinder the movement of the item, suggesting, in this case, some degree of coordination. It must be noted that group transport is an extraordinary task to be performed by an invertebrate. Even among vertebrates, group transport is only known among humans, dolphins, whales, and some canids (Moffett in press). Among invertebrates, the only other reported case of group transport is represented by the ants (Moffett in press).

Another feature apparently unique to *A. binotata* which may also result from the special architecture of its nests is its nomadic habit that leads to the periodic relocation of its colonies. The nests of other non-territorial permanently social species, which are usually expanded and occupied by more than one generation of spiders, are three-dimensional structures that are probably expensive to build and whose prey capture efficiency does not appear to depend on their invisibility. The two-dimensional nests of *A. binotata*, on the other hand, may be less expensive to rebuild and, most importantly, they appear to critically depend on their invisibility to trap prey. Such invisibility can best be achieved by rebuilding the nest in a new and debris-free locality.

The observation that egg laying is universal in *A. binotata* (Table 1) illustrates perhaps to an extreme a feature common to non-territorial, permanently social spiders which critically differentiates them from the most highly social insects: a lack of reproductive castes (Buskirk 1981; Darchen & Delange-Darchen 1986). Even though competition over resources leading to differences in reproductive success are not entirely absent

in social spiders (Riechert 1985; Seibt & Wickler 1988; Vollrath 1986; Rypstra in press), social spider colonies critically contain multiple reproductives of both sexes that can mate among themselves to produce subsequent generations. This leads to mating within colonies and to the highly subdivided population structure that characterize non-territorial permanently social species (Lubin & Crozier 1985; Smith 1986; Main 1988; Roeloffs & Riechert 1988; Avilés 1992). In contrast, perpetual inbreeding is rare or absent among the eusocial insects in which nuptial flights result in the crossing of individuals from different nests (Wilson 1971). Evidence that *A. binotata* has followed the route of other non-territorial permanently social spiders in developing strong population subdivision leading to intercolony selection and female-biased sex ratios will appear elsewhere.

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DNA SEQUENCE DATA INDICATES THE POLYPHYLY OF THE FAMILY CTENIDAE (ARANEAE)

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ABSTRACT. Mitochondrial DNA fragments comprising more than 400 bases of the 16S rDNA from nine spider species have been sequenced: *Cupiennius salei*, *C. getazi*, *C. coccineus* and *Phoneutria boliviensis* (Ctenidae), *Pisaura mirabilis*, *Dolomedes fimbriatus* (Pisauridae), *Pardosa agrestis* (Lycosidae), *Clubiona pallidula* (Clubionidae) and *Ryuthela nishihirai* (syn. *Heptathela nishihirai*; Heptathelidae: Mesothelae). Sequence divergence ranges from 3–4% among *Cupiennius* species and up to 36% in pairwise comparisons of the more distantly related spider DNAs. Maximally parsimonious gene trees based on these sequences indicate that *Phoneutria* and *Cupiennius* are the most distantly related species of the examined Lycosoidea. The monophyly of the family Ctenidae is therefore doubted; and a revision of the family, which should include DNA-data, is needed.

Cupiennius salei (Ctenidae) is one of the most extensively studied species of spiders (see Lachmuth et al. 1985). The phylogeny of the Ctenidae, a mainly South and Central American family, is poorly understood; and systematists propose highly contradicting views on its classification and phylogenetic placement (see e. g., Lehtinen 1967; Bücherl 1969). Coddington & Levi (1991) have recently questioned the monophyly of the Ctenidae, showing that the available information about taxonomically useful characters is still meager and fragmentary.

In recent years the value of DNA sequence data for taxonomic and phylogenetic research has become increasingly clear. DNA sequences contain a nearly inexhaustable quantity of information and may provide valuable insight allowing the evaluation of groups whose phylogeny is largely unresolved by morphological and other data (Kocher et al. 1989; Gatesy et al. 1992; Cunningham et al. 1992; review: Fernholm et al. 1989). Moreover, sequencing DNA—above all mitochondrial DNA (mtDNA; mainly maternal inheritance, lack of recombination)—has specific advantages over other techniques of genetic comparisons such as DNA/DNA hybridization or isoenzyme analysis: e. g., greater resolving power over a hierarchical range of intraspecific to intergeneric comparison and easy comparability with sequences from other species (see also Wilson et al. 1985). The polymerase chain reaction (PCR, Mullis & Faloona 1987; Saiki et al. 1988) is a fast alternative to conventional cloning to get a high copy number of the DNA segment of interest. The PCR depends on the availability of oligonucleotides that specifically bind to the flanking sequences of this DNA segment. These oligonucleotides serve as primers for a polymerization reaction that copies the segment *in vitro*. The PCR-product obtained is suitable for direct sequencing.

The principal aim of the present study was to elucidate the phylogenetic position of the family Ctenidae within the Lycosoidea *sensu* Homann (1971), using four ctenids, two pisaurids, one lycosid, one clubionid and one liphistiomorph spider. Specific PCR-products were obtained by using primers for the mitochondrial 16S ribosomal DNA, designed according to those used by Cunningham et al. (1992). The molecular data largely agree with the conclusions drawn from morphological taxonomy. The most intriguing and surprising result of our study is the indication of a considerable phylogenetic distance between *Cupiennius* and *Phoneutria*.

METHODS

Animals and DNA extraction.—Table 1 lists the animals investigated in this study. In the bigger spiders, muscle tissue was dissected out of the femora; for the smaller ones, the complete prosoma and legs were used to extract DNA. Tissues were put into a digestive solution (70 mM NaCl, 10 mM Tris-HCl pH 7.4, 25 mM EDTA pH 8.0, 0.9% SDS, 6 μg/ml Proteinase K), and incubated for 2–8 h in a water bath at

Table 1.—Systematic position and geographical origin of the spiders investigated. The number of individuals that were sequenced is given in parentheses.

Spider classification	Geographical origin
Mesothelae	
(1) *Ryuthela nishihirai* (Haupt 1979)	Japan
Opisthothelae	
Clubionidae	
(1) *Clubiona pallidula* (Clerck 1757)	Austria
Lycosoidea	
Ctenidae	
(1) *Cupiennius salei* (Keyserling 1876)	Mexico
(2) *Cupiennius getazi* Simon 1891	Costa Rica
(1) *Cupiennius coccineus* F. Pickard-Cambridge 1901	Costa Rica
(2) *Phoneutria boliviensis* (F. Pickard-Cambridge 1897)	Costa Rica
Lycosidae	
(2) *Pardosa agrestis* (Westring 1862)	Austria
Pisauridae	
(2) *Dolomedes fimbriatus* (Clerck 1757)	Austria
(1) *Pisaura mirabilis* (Clerck 1757)	Austria

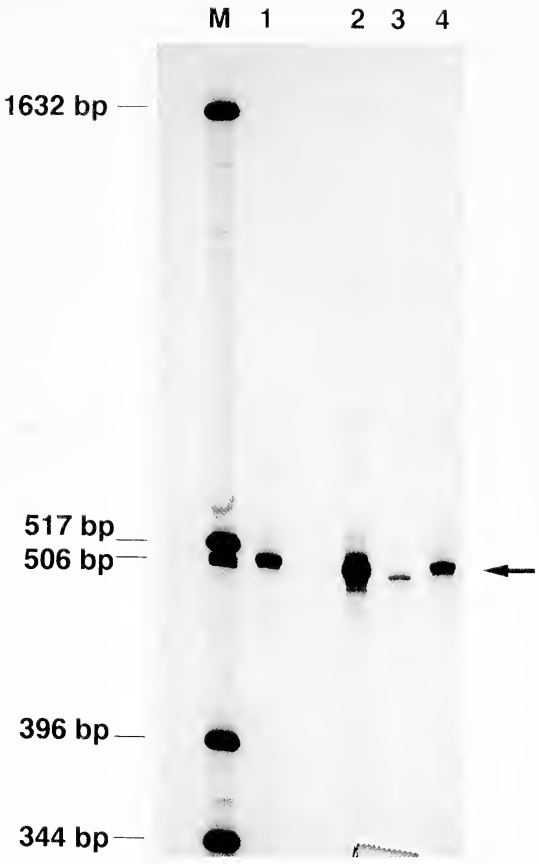

Figure 1.—Products of a radioactively labelled PCR amplification of a mt16S rDNA fragment. M = marker; 1 = *Cupiennius getazi*; 2 = *Pardosa agrestis*; 3 = *Clubiona pallidula*; 4 = *Dolomedes fimbriatus*. Arrow indicates the main products.

50 °C. Proteins were then precipitated with 5 M potassium acetate and RNA was digested by RNAse A (125 μg/ml; 15 min, 37 °C). DNA was precipitated with 60% v/v isopropanol (10 min, −20 °C), pelleted by centrifugation at 15,000 rpm for 20 min at 4 °C, washed with 400 μl of 70% ethanol, dried at 45 °C and resuspended in 20–40 μl TE buffer (10 mM Tris-HCl pH 8.0, 1 mM EDTA pH 8.0). The DNA preparation was stored at −20 °C.

Amplification and sequencing of rDNA.—The mt16S rDNA fragment was amplified using PCR with mt16S rDNA primers as designed by Cunningham et al. (1992), but with terminal extensions for Sac I restriction endonuclease (16sar: 5′–ATAGAGCTCCCATGGCGCCTGTTTATCAAAAACAT-3′ and 16sbr: 5′-ATAGAGCTCCCATGGCCGGTCTGAACTCAGATCACGT-3′). For the amplification assay 90–700 ng DNA and 2.5 units of DNA polymerase from *Thermus aquaticus* (Taq, Stratagene) were incubated in 100 μl of PCR buffer (Stratagene) with each of the four deoxynucleoside triphosphates (50 μM) and the primers (0.4 μM). For radioactive PCR 2-2.5 μCi alpha–^{32}P–dATP was added. The thermal profile for 40 cycles was as follows: (1) DNA melting for 1.5 min at 94 °C, (2) annealing for 2 min at 56 °C and (3) polymerization for 2 min at 72 °C. The product was electrophoresed on a 5% polyacrylamide gel (bisacrylamid : acrylamid 1:30; 8 M urea). Upon autoradiography of the gels the band of expected size was excised and a small piece was used for reamplification in 200 μl of buffer (concentration as above, without alpha–^{32}P–dATP). DNA was purified by the Geneclean II-kit (Bio 101) procedure according to the manufacturer's instruction. The template was then sequenced by the dideoxy chain termination

```
                                                                                                    60
Ryuthela        GTTGGTAATA AAAAATCTTA CCTGCTCCCT GCTATAAGTT AATAGCCGCA GTATTATGAC
Dolomedes       AGAAA.T..T ..T.G.AAA. T......AA. .AA.ATT-.A .........- -ATA------
Pisaura         AGAAA.T..T ..T.G.AAA. T......AA. .A..A.T-.C .........- -AT.------
Pardosa         AGAAT....T ..T...AAAT .......AA. .A-.A.T-.A .........- -.T.------
C.salei         AGAAA....T ..T.G.AAA. T......AA. .A.T..T-.A .........- -.TA------
C.getazi        AGAAA....T ..T.G.AAA. T......AA. .A.T..T-.A .........- -.T.------
C.coccineus     AGAAA....T ..T.G.AAA. T......AA. .A.T..T-.A .........- -.T.------
Phoneutria      A-AAA.T.AT ..T.G.AAG. T......AA. .A-.A.T-.A .......... -ACA------
Clubiona        AGATT.T.AT ..T.G.A.A. T......AA. .AAT.-T-.A .........G A.T.------
Psalmopoeus     A.GCT.C.C. TTT.G.AAG. .....A.AA. .A..C-T-.A .........T CAT-------

                                                                                                   120
Ryuthela        TGTGCTAAGG TAGCATAATC ATTTGTCTTT TAAATGAGGT CTGGAATGAA GGGTTTGATC
Dolomedes       .......... .......... .......... ...T.A.A.A ..A...CA.. A.A...A.-.
Pisaura         .......... .......... .......... ...T...A.A ..A...CA.. A.A...A.-.
Pardosa         .......... .........A .......... ...T.A.A.A ..A...CA.. A.....A.-.
C.salei         .......... .........A .......... ...T.A.A.A ..A...CA.. A.A...A.-.
C.getazi        .......... .........A .......... ...T.A.A.A ..A....A.. A.A...A.-.
C.coccineus     .......... .........A .......... ...T.A.A.A ..A...CA.. A.A...A.-.
Phoneutria      C......... ...T.....A .C........ ...T.A.A.A .-AA..CA.. A.A...A.-.
Clubiona        A......... .......... ...C...... ...T...A.A ..A...CA.. A.A..AA.-.
Psalmopoeus     .......... .....C...A .A.A.C..A. ...T..TA.G A...C..... A...C.A.-.

                                                                                                   180
Ryuthela        GAAGAAAGTC CTGTCTCTTT ATTATTTGGT -GAATTAAAT TAGCTAGTAA AAAGGCTAGT
Dolomedes       ATTT...T.A A.T.T.TAAA TC..A..AT. TA.....TT. ..AA.-.... ...AA.ATT.
Pisaura         TTTT...T.A A.A.T.TAAA T....AATT. TA.....TC. ..AA.-.... ....A.ATT.
Pardosa         ATCTC..T.A A.A.T.TA.A .GA.AC.TT. TA.....TT. ..AT.-.... ...AA.A.T.
C.salei         ATCTT..T.T A.T...TAAA T....C.AT. TA.....TC. ..AA.-.... ....A.ATT.
C.getazi        ATTTT..T.T A.T.T.TAAA T....A.AT. CA.....TC. ..AA.-.... ....A.ATT.
C.coccineus     ATCTT..T.T A.T.T.TAAA T....C.AT. TA.....TC. ..AA.-.... ....A.ATT.
Phoneutria      ATTTT...A. A...AA-ACA ....CA.AT. TA..C..TT. ...T.TT.C. ...AAAA.C.
Clubiona        ATTTT..T.A T.T.A.T..A .A..A..AT. AA....TTCC ..AA.-.... ....A.ATT.
Psalmopoeus     ATGA.GCT.T ..T.A.TA.A .AA..GAAT. GA...T.GCA .GAAA-.... ....A..TTA

                                                                                                   240
Ryuthela        ATAGGCCTGA AAGACGATAA GACCCTATTA AGCTTAATTT TTAAAATTTT ACTGGGGCGG
Dolomedes       ...TTATA.. .......... ........CG .A...TTAC. ...G--..AA .......TA.
Pisaura         ...ATTAA.. .......... .........G .A...T-AC. ...G--...A .......TA.
Pardosa         T.TAAAAA.. .......... ........CG .A...T-AC. ...G--...A .......AA.
C.salei         ..CTAATA.. .......... ........C. .A...T-AC. ...G--..AA ........A.
C.getazi        ..CTAATA.. .......... ........C. .A...T-AC. ...G--..AA ........A.
C.coccineus     ...TAATA.. .......... ........C. .A...T-AC. ...G--..AA ........A.
Phoneutria      ...CAAAAA. .......C.. .........G .A....-AC. ...G--..CA ........A.
Clubiona        .C.ATATA.. .......C.. .........G .A....-AC. A.TG--..AA ........A.
Psalmopoeus
```

Figure 2.—Multiple alignment of the mt16S rDNA sequences of the nine spider species investigated. Periods represent nucleotide identity with the reference sequence *Ryuthela nishihirai*. Dashes indicate positions where gaps were introduced to obtain maximal alignment. Highly conserved sequences in mt16S rDNA (as marked in Fig. 3) are underlined. *Psalmopoeus* sp., a theraphosid spider is included in this figure but was only partially sequenced and not taken into further consideration in this paper.

method of Sanger et al. (1977) using a Sequenase kit (U. S. Biochemical) as described in the protocol of the manufacturer. Sequencing was performed in both directions with the primers also used for the PCR. Sequencing reactions were electrophoresed on 7.5% polyacrylamide gels for 2–7 h (Sambrook et al. 1989).

Data analysis.—Sequence data were aligned

```
                                                                                                300
Ryuthela        TAGGATAAGA TTATAATCTT ATCCATAATG GTTGATATTT ATTGACCCAA TTTTATTGAG
Dolomedes       .TAAT...-- ....T..T.. .ATTTA-.AT AAAATCT.AA TAA....T.. .A.A...A.T
Pisaura         .TAAT...-- ....T..T.. .ATA.A-.AT AA.TT..AAA T.C....T.. ...A...A.T
Pardosa         .TAAT...-- ....C..T.. .AT-.....T AAAT...CAA T......T.. .AC....A.C
C.salei         .TAAT...-- ......CT.. .ATT..T..T AAATTC..AA -.A....T.. .A.A...A.T
C.getazi        .TAAT...-- .......T.. .ATT..T.AT AAATT.GAAA T.A....T.. .A.A...A.T
C.coccineus     .T.AT...-- .......T.. CATT..T.AT .AATT.CAAA C.A....T.. .A.A...A.T
Phoneutria      .T.AT...-- AA..-..... .ATT.C.T.T TAA--C.AAA TA.....T.. .CCA...A.T
Clubiona        .TAA....-- ...AT..T.. ..TT.CT..T AA.T.ATAAA T---.T.T.. .A.....A.T
Psalmopoeus                                                  TTTA.C. .C..CGATTA

                                                                                                360
Ryuthela        GGTAAGATAA AGCTACTATA GGGATAACAG CTTAATTTTC CTTTGAAGAT CTTATTTATT
Dolomedes       TTC.TA..C. ..T...CG.. .......... .G....AAAA T.C.T..... ........AA
Pisaura         TAA.TA..T. ..T...C... .......... .G.....AAA T...TT.... .......GAA
Pardosa         AA..TA..T. ..T...CG.. .......... .G....AAAA T..CT..... ........AA
C.salei         TA.TTA..C. ..T....G.. .......... .G....AAAA T...A..... ......A.AA
C.getazi        TACTTA..T. ..T....G.. .......... .G....AAAA T...A..... ......A.AA
C.coccineus     TAATTA..C. ..T....G.. .......... .G....AAAA T...A..... ......A.AA
Phoneutria      TAA..A..C. ..T...C... .......... .G....AA.T A.C.A...C. ..C..AC.AA
Clubiona        AAA------. ..T...C... .......... .A....AAAT A...A..... .....AC.AA
Psalmopoeus     TAAT.C.CC. ..T...CGC. .......... .AC...C..T T.CAAG...C .....CC.AA

                                                                                                420
Ryuthela        GGAAAGTTTG AGACCTCGAT GTTGAATTAA AGTACCTTAT AGGCGCAGTA GGCTA-TAAA
Dolomedes       AT....A... C......... .....T.... TAA-...A.. TCA....A.. .TAA...T..
Pisaura         ATTT..A... C......... .....T.... TT.-...A.. TTA....A.. .TT....T..
Pardosa         AT....A... C......... .....T.... TAA-...A.. TAA....A.. .TTA...T..
C.salei         AT....A... C......... .....T.... TT.T...A.. TAA....A.. .AAA...T..
C.getazi        AT....A... C......... .....T.... TT.T...A.. TTT....A.. .AAA......
C.coccineus     AT....A... C......... .....T.... TT.T...A.. TAA....A.. .AGA...T..
Phoneutria      AA.T..A... C......... .......... TAAT.-.A.. TT.....A.. .CAA..A...
Clubiona        TAT..TA..A T......... .......... TAA-...ATA TTAT...A.. ATTAT.A...
Psalmopoeus     AA....A..A T......... .......... -.ATT..CC. TAAA...AAG CTTA.GA...

                                                  446
Ryuthela        GGAAGTCTGT TCGACTTTTA AATCTT
Dolomedes       .......... .......... ..AAA.
Pisaura         .......... .......... ..AAA.
Pardosa         .......... .......... ..AAA.
C.salei         .......... .........G ...AA.
C.getazi        .......... .......... ...AA.
C.coccineus     .......... .......... ...AA.
Phoneutria      .A........ .......... ..AAA.
Clubiona        .......... .......... ..AAA.
Psalmopoeus     .A........ .......... ..C.-.
```

by CLUSTAL V (Higgins et al. 1991). Pairwise alignment and calculation of percent differences was carried out by MICROGENIE (Queen & Korn 1983). The data was subjected to DNAPARS and DNABOOT of PHYLIP 3.4 (Felsenstein 1991). Gaps comprising more than one site were treated as missing data, and thus played no role in phylogenetic reconstruction.

Aligned sequences were fitted into available secondary-structure models from Gutell & Fox (1988).

RESULTS

Initially we tried to use the conserved primers of Kocher et al. (1989) to amplify a fragment of the cytochrome b gene of spiders. These primers

Table 2.—Percentage of base identities of the mt16S rDNA between the investigated spiders. The values are rounded off.

	Ryu.	*Phon.*	*Club.*	*Pard.*	*Pisa.*	*Dolo.*	*C.coc.*	*C.get.*
Cupiennius salei	66	79	80	87	86	90	97	96
Cupiennius getazi	67	79	80	86	88	90	96	
Cupiennius coccineus	65	79	80	87	88	89		
Dolomedes	67	81	82	88	90			
Pisaura	68	78	81	87				
Pardosa	67	79	79					
Clubiona	65	77						
Phoneutria	64							

proved to be unsuitable for our experimental animals, however. In a second attempt we used primers designed according to those used by Cunningham et al. (1992) to amplify and study mt16S rDNA in crabs. This approach led to the amplification of some fragments but suffered from the poor reproducibility of the results. We therefore chose to apply a two step amplification procedure. In a first step, PCR amplification was performed with simultaneous radioactive labelling of the polymerized DNA. The products were separated on polyacrylamide gels and autoradiographed (Fig. 1). In a second step DNA material of the major amplification product (about 500 bp, see Fig. 1) was gel-extracted and subjected to a non-radioactive PCR amplification. A unique distinct band was obtained which was subjected to dideoxy sequencing after gel-extraction (see Methods).

Some bands of the expected size were also eluted from the first experiment. The DNA obtained from them was partially sequenced after reamplification and the identity of its main band with mt16S rDNA confirmed.

The DNA sequences of the nine spider species investigated in this study are shown in Fig. 2. The length of the sequenced fragment varies between 421 (*Clubiona pallidula*) and 444 bases (*Ryuthela nishihirai*). The percentage of identities in sequence is 64% or higher in all pairwise comparisons (Table 2); and a full alignment was reached, assuming a few small deletions only (Fig. 2). This clearly indicates the homology of the sequences determined.

In four cases, two individuals of the same species were examined (*cf.* Table 1) and as expected from previous work on tetragnathid spiders (Croom et al. 1991) no intraspecific variation was found. Interspecific variation between the three *Cupiennius* species is low (3–4%), whereas intergeneric differences vary conspicuously, ranging from 10–36% (Table 2).

The percentage of A and T along the sequenced DNA fragment is high (75.0–78.6%) in all species investigated except the "primitive" liphistiomorph spider *Ryuthela nishihirai* (66.7%). Similar results were obtained by Cunningham et al. (1992) for Crustacea (the "primitive" *Artemia salina*: 63% AT; the highly evolved king crabs *Pagurus* spp.: about 73% AT). In insects data is only available for highly evolved species such as *Drosophila yakuba* (Clary & Wolstenholme 1985) and *Aedes albopictus* (HsuChen et al. 1984). Both of these insects have a very high percentage of AT (about 76%), too. Possibly, an increase in the percentage of A and T is a general trend in arthropod phylogeny (*cf.* Clary & Wolstenholme 1985).

Figure 3 presents an attempt to fit the partial sequence of *Cupiennius salei* rDNA into a generally accepted secondary structure model for animal mt16S rRNA (Gutell & Fox 1988). The resulting secondary structure is very similar to that of the mt16S rRNA of both *Drosophila yakuba* and *Aedes albopictus* which are the only arthropods studied in this regard. In *C. salei* generally well conserved sequences (marked in Fig. 3) take the same positions relative to the overall secondary structure of mt16S rRNA. In addition these sequences show no variation among the nine spiders examined (*cf.* Fig. 2). Thus we conclude that a fragment of mt16S rDNA indeed has been sequenced.

One of the several most parsimonious trees constructed by DNAPARS is shown in Fig. 4. When changing the order of the DNA sequences in the input file the same result was obtained in most cases. Other trees varied slightly regarding the relationships between *Cupiennius*, *Pardosa* and the pisaurids. In no case was *Phoneutria*

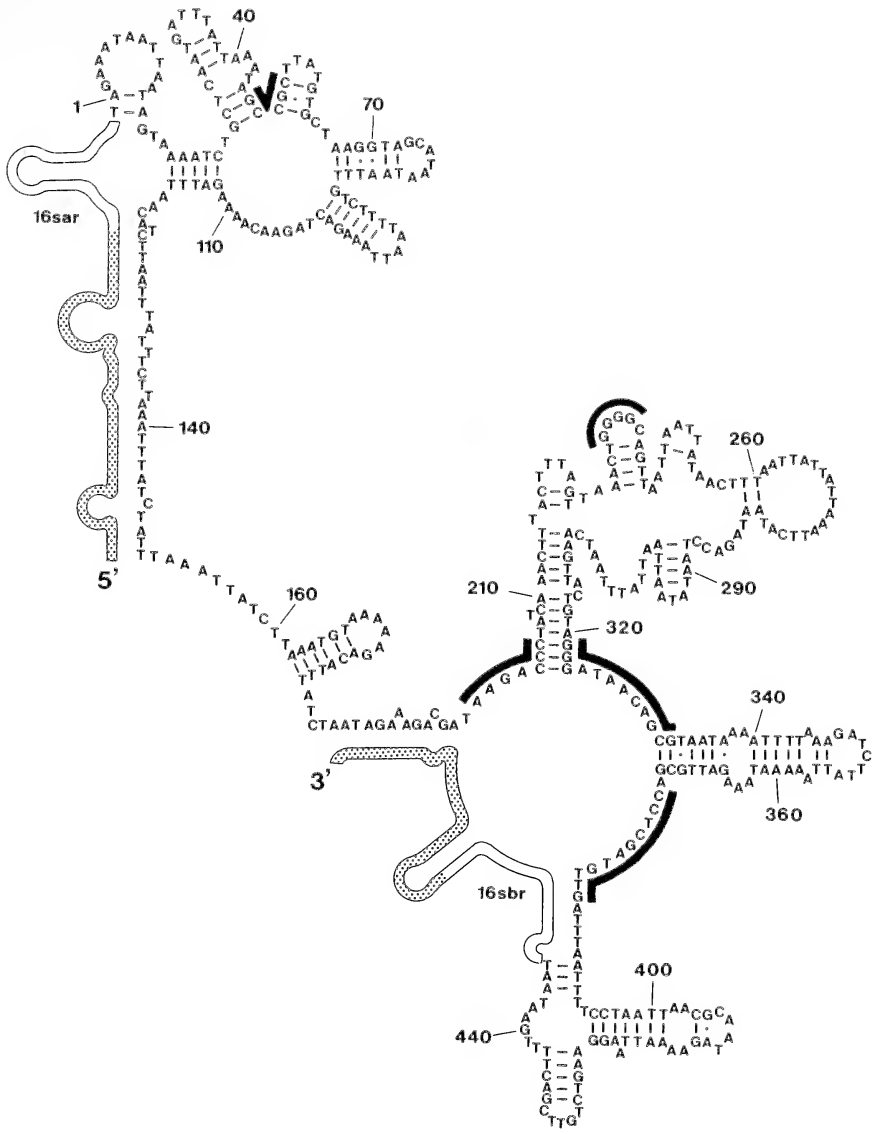

Figure 3.—Mitochondrial DNA of *Cupiennius salei* folded to show the secondary structure of the sequenced 16S ribosomal RNA for which it codes. Dashes represent Watson-Crick pairings, dots represent the weaker hydrogen bonds between T and G or A and G. Grey beams indicate the supposed secondary structure of the adjacent sequences, based on the model for *Drosophila yakuba* in Gutell & Fox (1988). 16sar, 16sbr (white beams): priming sites. Black lines indicate extremely conserved regions known to be almost identical in vertebrates as well as in *Escherichia coli*. Numbering as in Fig. 2.

interpreted as a sister group of *Cupiennius*. However, in a bootstrap analysis with 1000 replicates the three *Cupiennius* species were regarded monophyletic in 94% of the bootstrap estimates. This occurred only 19–54% in the other groups.

DISCUSSION

This communication presents the first extended analysis of spider mt16S rDNAs for phylogenetic studies. It is based on the PCR amplification of this gene fragment in nine spider species representing five families.

The similarity (64–97% identity) of the 421–444 bp long sequences in all cases indicates that homologous sequences have been determined from all nine species. Furthermore, the derived RNA sequences fit well into the conserved secondary structure of other animal mt16S rRNAs

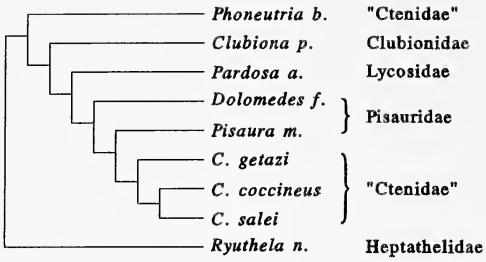

Figure 4.—Mt16S rDNA gene-tree based on the most parsimonious tree obtained in most cases when applying the DNAPARS program of PHYLIP 3.4 (Felsenstein 1991). Note the position of *Phoneutria* in relation to *Cupiennius*.

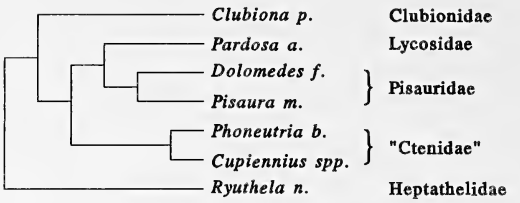

Figure 5.—Current view on phylogenetic relationships of the examined taxa, based on the cladistic hypothesis of Coddington & Levi (1991).

and highly conserved signature sequences of mt16S rRNA can be identified unambiguously. Finally, short sequences of this mt16S rDNA fragment and of a previously determined mt12S rDNA fragment (Croom et al. 1991) are successfully used as primers for the PCR amplification of large, adjacent parts of both rDNAs (R. J. Felber, pers. comm.).

Sequence variation is low when the three species of *Cupiennius* are compared (3–4%) whereas it varies between 10–23% among the Opisthothelae studied here (Table 2). This indicates that sequences of the mt16S rDNA may be useful for studies of spider phylogeny at the family and higher taxonomic levels.

Although limited, the data presented here reveal an intriguing result: In all of the maximum parsimonious gene trees *Phoneutria* was more distantly related to *Cupiennius* than *Pardosa* and the two pisaurids. This sheds doubt on the available classification of both genera—*Phoneutria* and *Cupiennius*—within the Ctenidae and indeed on the monophyly of this family, which was established by Keyserling in 1877. The monophyly of the included genera has mainly been based on the following morphological characters: (1) ecribellate spiders with (2) an eye-formula quite peculiar to them among (3) the two-clawed spiders (Pickard-Cambridge 1897; Bücherl et al. 1964). These are all characters which also occur in other families and therefore cannot be considered as strong synapomorphies. Depending on the position of the nominal genus *Ctenus*—which could not be investigated in this project—either a new family for *Cupiennius* (*Ctenus* closely related to *Phoneutria*) or for *Phoneutria* (*Ctenus* closely related to *Cupiennius*) may well be appropriate. One obvious next step is therefore the examination of the nominal species of the Ctenidae.

The critical evaluation of this far-reaching implication of our study asks for answers to several questions. One of these concerns the identification of *Phoneutria* species, which is still a problem. Many Neotropical taxa are still undescribed (Coddington & Levi 1991) and there is no recent revision of the genus. The two female individuals studied by us were identified using the key of Bücherl (1969). Their genitalia were dissected, treated with KOH and then compared with illustrations provided by Schiapelli & Gerschman (1973) and by Valerio (1983). Given the species specificity of spider genitalia, our morphological study makes it highly probable that the spiders in question belong to the species *Phoneutria boliviensis*. Another question is the possibility of contaminations. However, DNA was extracted from both individuals independently. Separate amplification and up to threefold sequencing of some segments led to absolutely identical results. Contaminations are therefore considered a very unlikely reason for the surprising position of *Phoneutria* in the gene tree derived from our DNA analysis.

Except for the apparent polyphyly of the Ctenidae, the maximum parsimony tree proposed in Fig. 4 does not allow any further conclusions on spider phylogeny. Details such as the relationships between the three *Cupiennius* species or between *Pisaura* and *Dolomedes* should not be given too much weight. According to the low values obtained by bootstrap analysis these relationships are not significant (there is significant evidence for the monophyly of a group if it occurs in at least 95% of the bootstrap replicates: Felsenstein 1991). From a morphological point of view *Phoneutria* belongs to the monophylum of spiders characterized by at least one pair of secondary eyes with a grate-type tapetum (Homann 1971). *Clubiona* (with a canoe-shaped tapetum) on the other hand does not belong to this monophylum and should therefore branch off deeper

in the tree (Fig. 5). There is not sufficient data to resolve this discrepancy, however. We now rather need a comprehensive examination of additional genera, including both molecular and morphological information.

ACKNOWLEDGMENTS

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TAXONOMIC NOTES ON THE GENUS *ARCHITIS* (ARANEAE, PISAURIDAE) AND STATUS OF THE GENUS *SISENNA* SIMON

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ABSTRACT. *Dyrines tenuipes* (Simon) is a senior synonym of *Architis vilhena* Carico. *Thanatidius proximatus* Mello-Leitão (=*Thanatidius parahybensis* Mello-Leitão) is a junior synonym of *Architis tenuis* Simon. *Sisenna* Simon is a junior synonym of the genus *Architis. Sisenna helveola* Simon, the only species placed in *Sisenna,* is redescribed and figured as *Architis helveola* (Simon). A lectotype of the latter species is designated. Errata in a previous publication are noted.

During a survey of types of some lesser known pisaurid genera in the New World, three misplaced species were found to belong to the pisaurid genus *Architis.* This paper reports on the taxonomic status of these species.

***Dyrines tenuipes* (Simon).**—*Dyrines tenuipes* (Simon 1898[b]:18) (transferred from *Drances* by Petrunkevith 1911:543) is a senior synonym of *Architis vilhena* Carico (1981:150, figs. 1, 10, 22, 23) based on the examination of six male syntypes, #5408, deposited in the Muséum National d'Histoire Naturelle, Paris, collected from Cameta, Para, Brazil by Mathan. The female was described by Carico (1989:224, figs. 6, 7). The correct name of this species is, therefore, *Architis tenuipes* (Simon). NEW SYNONYMY.

***Thanatidius proximatus* Mello-Leitãao.**—The holotype of *Thanatidius parahybensis* Mello-Leitão (1924) from Campino Grande, Paraíba, Brazil, collected by Tranquilino Mello-Leitão (specimen #88, labelled *Pisaurina parahybensis* Mello-Leitaao), in the Museu Nacional do Rio de Janeiro, is a penultimate female collected just prior to ecdysis. The adult epigynum is clearly visible through the old cuticle, and close examination reveals the characteristic features of *Architis tenuis* Simon.

Mello-Leitão described this specimen first (1920) as *T. proximatus* and later (1924) as *T. parahybensis.* Roewer (1954) first reported the objective synonymy. Bonnet (1959) lists only *T. parahybensis.* Both are junior synonyms of *Architis tenuis* Simon. NEW SYNONYMY.

Errata in previous publication.—In my revision of the genus *Architis* (Carico 1981), labels for epigyna of two species were interchanged. Figures 26, 27 should be labelled *A. nitidopilosa,* and figs. 32, 33 should be labelled *A. tenuis* as was reported by Sierwald (1989). Additionally, fig. 6 should be labelled *A. cymatilis.*

Sisenna helveola.—The type of the monotypic genus, *Sisenna, S. helveola* Simon, is congeneric with the genus *Architis.* Therefore, the genus *Sisenna* is a junior synonym (NEW SYNONYMY) of the pisaurid genus *Architis.* This conclusion differs from that of Sierwald (1990) who placed *Sisenna* tentatively in her "*Trechalea* genus-group," which I regard as the family Trechaleidae.

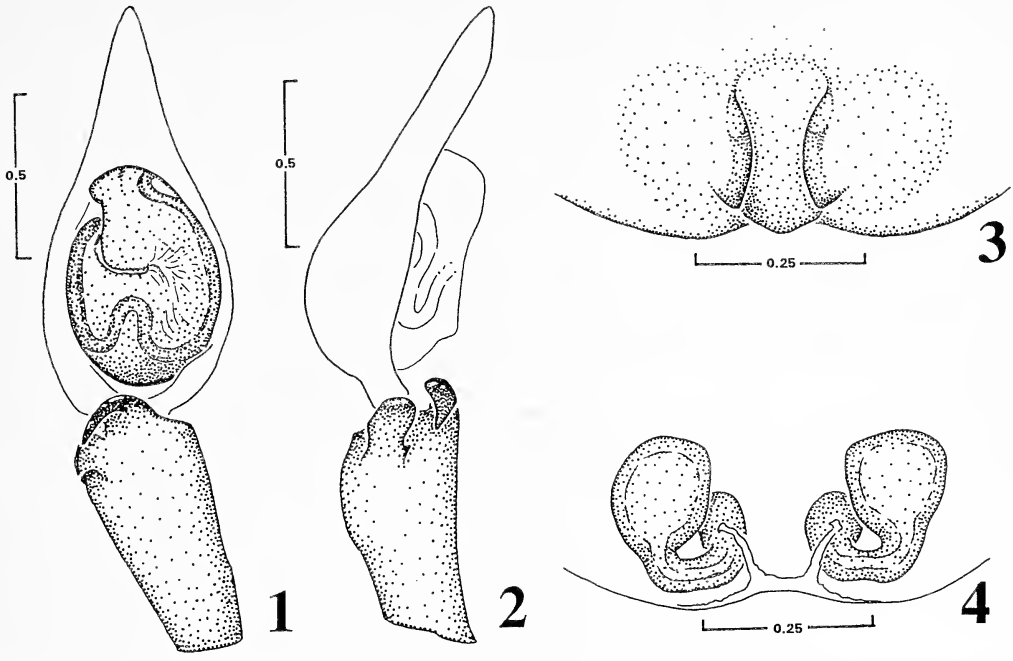
Below is the redescription of *A. helveola,* which becomes the tenth known species in the Neotropical genus *Architis,* four of which were described by Simon. It is interesting to note that Simon originally placed his four species into three different pisaurid genera which he also described: *Architis* (two species), *Drances* (one species) and *Sisenna* (one species). The male genitalia of all *Architis* species are quite similar while the eyes and body shape show a greater range of variability. Apparently Simon placed more emphasis on these non-genitalic characters in his generic definitions.

Architis helveola (Simon)
Figures 1–4

Sisenna helveola Simon, 1898[b]:12 (n. sp.). Simon, 1898[a]: 292, figs. 290, 291 (n. gen.).

Sisenna helvola, Roewer, 1954:123. Bonnet, 1955–1959:4065.

Type.—Male syntype from São Paulo Olivença, Amazonas, Brazil, designated herein as lectotype. Female paralectotype from same locality.



Figures 1–4.—Genitalia of *Architis helveola*: 1, 2, right male palpus; 1, ventral view; 2, retrolateral view; 3, 4, epigynum; 3, ventral view; 4, dorsal view. Scales are in mm.

This part of the Mathan Collection identified as #6895 in the Muséum National d'Histoire Naturelle, Paris. Examined.

Diagnosis.—This species resembles *Architis tenuis* and *A. nitidopilosa* in the AE row configuration (see Carico 1981, fig. 9). It differs from the latter two species in details of the genitalia, particularly the tibial apophysis of the male and the ventral view of the female epigynum, and by the lack of short, stout spines on the ventral surface of coxae I and II.

Description.—(Measurements in mm) *Male lectotype:* Carapace low, no pattern on cream ground color; each eye individually ringed in black; length 2.9, width 2.4. Sternum length 1.45, width 1.50, unmarked; labium length 0.46, width 0.42, unmarked, rounded anteriorly. Eye measurements: AE row 0.83, PE row 0.80; ocular quadrangle height 0.42, width posterior 0.40, width anterior 0.34; diameters PLE 0.16, PME 0.16, ALE 0.12, AME 0.14; interdistances PLE-PME 0.18, PME-PME 0.12, ALE-AME 0.24, AME-AME 0.08. Clypeus height 0.05 (ALE) or 0.22 (AME), width 1.02. Legs I–II–IV–III, unmarked with numerous long, dark macrosetae. Measurements are given in Table 1.

Abdomen narrow, mostly covered with irregular white pattern on cream ground color except for midventral area; patch of dark hairs on anterodorsal margin, length 5.1. Palpus (Figs. 1, 2) with two tibial apophyses: ventral one curved and pointed apically, retrolateral one flat, curved towards cymbium with small point at base ventrally.

Female paralectotype: Carapace color and pattern as in male; length 3.0, width 2.5. Sternum

Table 1.—Leg measurements (in mm) for the male lectotype and the female paralectotype of *Architis helveola* (Simon).

	I	II	III	IV
Male				
Femur	5.45	5.2	3.5	4.4
Tibia-patella	7.4	7.0	4.25	4.65
Metatarsus	6.6	6.1	3.5	4.45
Tarsus	2.1	1.95	1.1	1.6
Total	21.55	20.25	12.6	15.1
Female				
Femur	4.9	—	3.4	4.1
Tibia-patella	6.75	—	4.0	4.55
Metatarsus	6.0	—	3.55	4.1
Tarsus	1.85	—	1.35	1.6
Total	19.5	—	12.3	14.35

and labium as in male. Abdomen pattern and hairs as in male, length 5.35. Sternum length 1.60, width 1.55, unmarked; labium length 0.55, width 0.50, unmarked, rounded anteriorly. Eye measurements: AE row 0.92, PE row 0.86; ocular quadrangle height 0.40, width posterior 0.45, width anterior 0.36; diameters PLE 0.17, PME 0.17, ALE 0.12, AME 0.13; interdistances PLE-PME 0.22, PME-PME 0.16, ALE-AME 0.33, AME-AME 0.11. Legs (II missing), color and macrosetae as in male, and the measurements are in Table 1.

Epigynum with openings medially, each under longitudinal ridge (Figs. 3, 4), pale and soft externally.

Natural history.—Unknown.

Distribution and material examined.—These male and female are the only known specimens.

Notes.—Bonnet (1955–1959:77) changed the spelling of this species as well as other "helveola" species of Simon to "helvola", because the latter is a more frequently used form. The "helveola" spelling does indeed seem to be a rare form (H. D. Cameron pers. comm.), but the spelling change is not justified according to the current International Code of Zoological Nomenclature.

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TWO NEW SPECIES OF THE GENUS *LYSSOMANES* (HENTZ) FROM THE CAPE REGION, B.C.S., MEXICO

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ABSTRACT. Two new species of the genus *Lyssomanes* Hentz from the Cape Region, Baja California Sur, are described and illustrated. ***Lyssomanes burrera*** n. sp. is similar to *Lyssomanes jemineus* Peckham, Peckham & Wheeler, and ***Lyssomanes pescadero*** n. sp. is similar to *Lyssomanes mandibulatus* F. O. P. Cambridge.

Sixty-one species of spiders from the Americas are included in the genus *Lyssomanes* Hentz (Galiano 1980, 1984) and ten of these species are present in Mexico: *L. jemineus* Peckham, Peckham & Wheeler 1889, *L. temperatus* Galiano 1980, *L. diversus* Galiano 1980, *L. malinche* Galiano 1980, *L. placidus* Peckham, Peckham & Wheeler 1889, *L. unicolor* (Taczanowski 1872), *L. deinognathus* Cambridge 1900, *L. mandibulatus* F. O. P.-Cambridge 1900, *L. elegans* F. O. Pickard-Cambridge 1901 and *L. spiralis* F. O. Pickard-Cambridge 1901 (Richman & Cutler 1988).

The genus *Lyssomanes* is primarily tropical with a high concentration of species in Brazil, but it has not been well studied in Mexico; and the possibility exists that there are many new species there (Galiano 1980). Mexico, from a biogeographical point of view, is considered to be as a transitional zone occupied by elements of a hybrid fauna of both Neotropical and Nearctic origin. There are strong endemic characteristics, but there are also affinities with the faunas of both South America and temperate North America (Halffter 1976).

This is the first record of the genus *Lyssomanes* from the peninsula of Baja California. We describe two new species: *Lyssomanes burrera* n. sp. is included in the *jemineus* group because of fringes of black setae on the tibia and tarsus and the long and divergent chelicerae of the males. The bulb of the palp has a cylindrical embolus ending in a sharp tip and its base has an apophysis. *Lyssomanes pescadero* n. sp. is included in the *viridis* group because it has very long and divergent chelicerae. The bulb of the palp is relatively simple, with its basal part of the embolus covered partial or wholly by a membranous sheath.

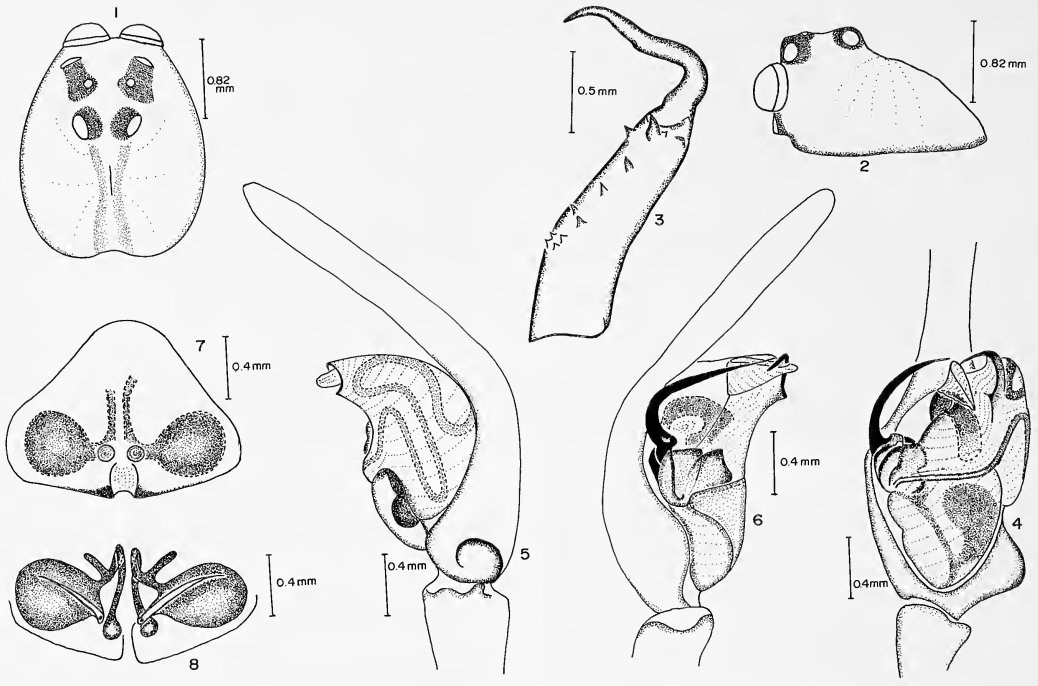
Lyssomanes burrera, new species
(Figs. 1–8)

Type.—Male holotype from low deciduous forest, 600 m elev., Cañon de la Burrera, Sierra de la Laguna, Baja California Sur (25 June 1992), A. Tejas and G. Navarrete. Two male and one female paratypes are from the type locality (25 June 1992, A. Tejas and M. Jiménez). One female paratype is from low deciduous forest, 753 m elev., Cañon de la Zorra, Sierra de La Laguna, (29 October 1987, M. Jiménez). The holotype and a female paratype will be deposited in the collection of the Instituto de Biológia, Universidad Autonoma de México, and three paratypes will be deposited in the arachnological collection of the Centro de Investigaciones Biológicas de Baja California Sur, A.C.

Etymology.—The specific name is derived from the type locality.

Diagnosis.—Members of *Lyssomanes burrera* n. sp. resemble *L. jemineus* Peckham, Peckham, & Wheeler in coloration and body shape, but can be separated from the other known similar species by the shape of the embolus, the number of teeth of the female chelicerae, leg spination, and the shape of the epigynum.

Males.—(n = 2). Total length 5.58–8.33 mm; prosoma 2.55–2.70 mm long, 1.95–2.15 mm wide and 1.25–1.75 mm high (Fig. 1, 2). Clypeus 0.20 high. Eye sizes and interdistances: AME 0.55, ALE 0.26–0.29, PLE 0.23–0.26, ALE-PME 0.18–0.20, PME-PLE 0.34–0.36, ALE-PLE 0.52–0.58. Eye row widths: first 1.08–1.14, second 1.00–1.06, third 0.60–0.64, fourth 0.82–0.84. Chelic-



Figures 1–8.—***Lyssomanes burrera*** n. sp. holotype male from Cape Region of Mexico: 1. dorsal view of the carapace; 2. lateral view of the carapace; 3. right chelicera; 4. ventral view of palp; 5. retrolateral view of palp; 6. prolateral view of palp; 7. ventral view of epigynum; 8. female dorsal view of epigynum.

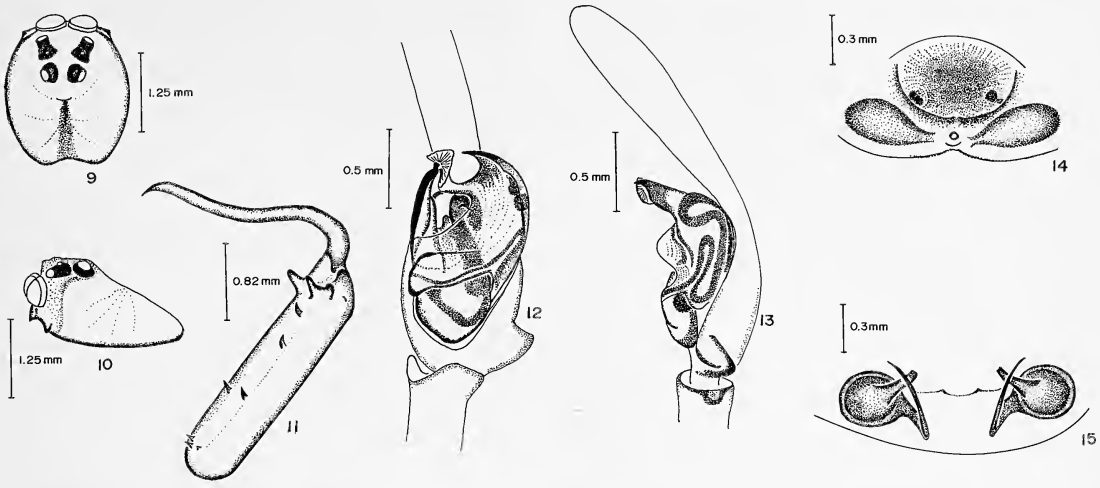
erae moderately long and divergent from the base. Anterior surface with 2–3 median spines and 4–7 dorsal spines. Promargin with four teeth, retromargin with six teeth and a small apophysis near the the fang (Fig. 3). Leg spination: Femora I-III d 1-1-1, p 0-1-1, r 0-1-1; IV d 1-1-1, p 0-0-1, r 0-1-1; Patella I-IV d 0-0-1; Tibia I p 0-1-1, r 0-1-1, v 2-2-2; II d 0-1-1, p 0-1-1, r 0-1-1, v 2-2-2; III d 1-0-1, p 0-1-1, r 0-1-1, v 0-2-2; IV d 1-0-1, p 0-1-1, r 0-1-1, v 0-1-0; Metatarsi I-II p 0-0-1, r 0-0-1, v 2-2-2; III p 0-0-1, r 0-0-1, v 2-2-1; Palpi: Femur 1.14–1.85, d 0-1-1, p 0-0-1, r 0-0-1; Patella 0.40–0.66, d 0-0-1, r 0-0-1; Tibia 0.56–0.64, d 0-0-8, p 0-1-1; Cymbium 1.50–1.76 (Figs. 4, 6).

Color in alcohol: Carapace light yellow with a longitudinal dark band. Ocular quadrangle light with the ALE, PME and PLE in black tubercles and rounded with white setae, clypeus yellow with lower edge orange red, setae on each side; anterior surface of the chelicerae dark yellow, inner side darker, sternum light yellow. Opisthosoma dorsally yellow with two green, longitudinal dark brown bands; venter yellow, spinnerets darker. Legs yellow without marks and stripes. First metatarsus curved and flattened on the sides and a little dilated dorsoventrally, blackish with iridescent shine and fringes of black setae above and below. Tibia I with fringe of black setae distally above and below. Palps yellow with distal part of the tibia orange yellow.

Living specimens are green in color, with white and orange-red ocular setae.

Female.—($n = 3$). Total length 6.50–8.00 mm. Carapace 2.50–2.60 long, 1.80–2.15 mm wide, 1.50–1.75 high. Clypeus 0.25. Eye sizes and interdistances: AME 0.50–0.55, ALE 0.26–0.28, PLE 0.14–0.23, ALE-PME 0.16–0.29, PME-PLE 0.34–0.59, ALE-PLE 0.42–0.95. Eye row widths: first 1.08–1.10, second 1.00, third 0.60–0.64, fourth 0.82. Leg spination: Femora I-III d 1-1-1, p 0-1-1, r 0-1-1; IV d 1-1-1, r 0-0-1; Patella II-IV d 0-0-1; Tibia I p 0-1-1, r 0-1-1, v 2-2-2; II d 0-1-1, p 0-1-1, r 0-1-1, v 2-2-2; III d 0-1-1, p 0-1-1, r 0-1-1, v 0-2-2; IV d 1-0-1, p 1-0-1, r 0-1-1, v 0-0-1; Metatarsi I-II p 0-0-1, r 0-0-1, v 2-2-2; III p 1-1-1, r 0-0-1, v 1-1-1; IV p 0-1-1, r 0-1-1, v 0-1-1. Epigynum (Fig.7, 8).

Color in alcohol: Light yellow, ocular quadrangle with lateral white and dorsal red setae, and long whitish setae around AME and ALE. Clypeus with iridescent setae and red orange setae on the sides. Chelicerae with three promarginal and five retrolateral teeth. Opisthosoma long



Figures 9–15.—***Lyssomanes pescadero*** n. sp. holotype male from Cape Region of Mexico: 9. dorsal view of the carapace; 10. lateral view of the carapace; 11. right chelicera; 12. ventral view of palp; 13. retrolateral view of palp; 14. dorsal view of female epigynum; 15. ventral view of epigynum.

and slender, with two longitudinal marks as in the males.

Habitat: Specimens were collected under leaves of mango and underside of wide leaves of riparian shrubs.

Range.—Known only from the type locality.

Lyssomanes pescadero, new species
(Figs. 9–15)

Types.—Male holotype from Rancho San Simón, Pescadero, Baja California Sur. (9 June 1992; A. Tejas, M. Jiménez and F. Cota). Eleven paratypes are from the same type locality. The holotype and a female paratype will be deposited in the collection of Instituto de Biología, Universidad Autónoma de México,and ten paratypes which will be deposited in the arachnological collection of the Centro de Investigaciones Biológicas de Baja California Sur.

Etymology.—The specific name is derived from the type locality.

Diagnosis.—Male specimens of *Lyssomanes pescadero* n. sp. resemble *L. mandibulatus* F. O. Pickard-Cambridge in shape and coloration, but can be separated from the other known similar species by the shapes of the bulb in lateral view, the median apophysis, and the embolus and by the number of cheliceral teeth and leg spination.

Males.—(n = 6). Total length 6.07–8.52 mm prosoma 2.94–3.62 mm long, 2.35–3.13 mm wide and 1.50–2.00 high (Figs. 9, 10). Clypeus 0.20–0.25 high. Eye size and interdistances: AME 0.50–0.60, ALE 0.23–0.26, PLE 0.19–0.23, ALE-PME 0.14–0.20, PME-PLE 0.28–0.36, ALE-PLE 0.44–0.60. Eye row widths: first 1.04–1.22, second 1.04–1.18, third 0.64–0.76, fourth 0.78–0.96. Chelicerae strong, very long and divergent from the base. Anterior surface with three basal spines and 19 distal spines. Promargin with one distal apical tooth and three small teeth and retromargin with five teeth, the apical tooth bifurcated and a small apophysis near the base of the fang (Fig. 11). Leg spination: Femora I-III d 1-1-1, p 0-1-1, r 0-1-l; IV d 1-1-1, p 0-1-1, r 0-0-1; Patella II-IV d 0-1-1; Tibia I p 0-1-1, r 0-0-1, v 2-2-2; II d 0-1-1, p 0-1-1, r 0-1-1, v 2-2-2; III d 0-1-1, p 0-1-1, r 0-1-1, v 0-2-0; IV d 0-1-1, p 0-1-1, r 0-1-1; Metatarsi I p 0-0-1, r 0-0-1, v 2-2-2; II p 0-0-1, r 0-0-1, v 2-2-2; III p 0-0-1, r 0-0-1, v 2-2-1; IV p 1-1-1, r 0-1-1, v 0-0-1; Palps: Femur 1.62–2.08, d 0-1-1, p 0-0-1, r 0-0-1; Patella 0.56–0.76, d 0-0-1; Tibia 0.69–0.89, d 0-0-1, p 0-1-1. Cymbium 1.32–1.55 (Figs. 12,13).

Color in alcohol: Carapace robust and sides prominent at the ocular area, dark yellow, with a longitudinal dark band. The carapace is bordered with a black line in darker specimens and with white setae around the eyes; ALE, PME and PLE on black tubercles, ocular quadrangle with white dorsal and lateral setae and an inner curved band of orange-red hairs; clypeus yellow with orange-red hairs on each side and a dark line under the median anterior eyes, border darker; anterior surface of the chelicerae darker yellow, fangs dark yellow, sternum and mouthparts shiny yellow. Opisthosoma light yellow with two dor-

sal longitudinal dark bands broken at the middle and two pairs of median black spots. In light specimens there are three pairs of black spots only. Spinnerets darker, venter yellow without marks. Legs yellow with gray lateral bands. First metatarsus and tibia with small fringes of black setae above and below. Palps yellow with the cymbium darker. Living specimens are green or yellow with shining orange red setae in the ocular area.

Female.—($n = 6$). Total length 5.58–9.01 mm. Carapace 2.94–3.62 long, 2.35–3.13 wide and 1.30–1.75 high. Clypeus 0.2–0.25 high. Eye size and interdistances: AME 0.55, ALE 0.23–0.26, PLE 0.19–0.23; ALE-PME 0.20–0.14, PME-PLE 0.30–0.34, ALE-PLE 0.48–0.56. Eye row widths: first 0.96–1.18, second 0.98–1.12, third 0.68–0.74 and fourth 0.76–0.90. Leg spination: Femora I-III d 1-1-1, p 0-1-1, r 0-1-1; IV d 1-1-1, r 0-0-1; Patella II-IV d 0-0-1; Tibia I p 0-1-1, r 0-1-1, v 2-2-2; II d 0-1-1, p 0-1-1, r 0-1-1, v 2-2-2; III d 0-1-1, p 0-1-1, r 0-1-1, v 0-0-2; IV d 0-1-1, p 0-1-1, r 0-1-1; Metatarsus I-III p 0-0-1, r 0-0-1, v 2-2-2; IV p 1-1-1, r 0-1-1, v 0-0-1. Epigynum (Fig. 14, 15).

Color in alcohol: Light yellow with orange-red setae between the eyes, dorsal and lateral sides of the ocular area with white setae, eyes surrounded by white setae. Clypeus with a band of white setae and red setae on each side. Cheliceral promargin with three teeth and retromargin with five teeth and two dorsal inner spines. Opisthosoma white with three pairs of green spots. Legs yellow, the metatarsi and tarsi darker. Living specimens are green or yellow, the ocular quadrangle with yellow setae.

Range.—Known from the type locality and from Cañon de la Burrera, Sierra de La Laguna, B. C. S.

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THE ORB-WEAVER GENUS *KAIRA* (ARANEAE: ARANEIDAE)

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ABSTRACT. Adult specimens of *Kaira* are rarely collected and the females are difficult to separate. The few specimens in collections represent 14 species, all American. Five species are new: *Kaira cobimcha* from southern Brazil; *K. dianae* from southeastern Peru; *K. erwini* from Peru; *K. shinguito* from northern Peru; *K. tulua* from Depto. Valle, Colombia. The female of *K. hiteae* is described and *Araneus sexta* is transferred to *Kaira*.

Haliger is a new synonym of *Kaira*, with *H. corniferus* a synonym of *K. altiventer*. *Kaira obtusa* and *Wagneriana minutissima* are synonyms of *K. gibberosa*. Doubtful synonyms are *Caira capra* of *K. altiventer*, and *Macpos monstrosus* of *K. gibberosa*.

In the past many authors named spiders without adequately illustrating them, and without comparison to other species in the same genus. The current approach is to name new species only as one aspect of a comprehensive revision of the entire genus, including the examination and comparison of old holotypes (vouchers for species names), and adequate illustrations of both sexes. While such revisions are required to make it possible to determine spiders, only a few revisions of Neotropical spiders are available.

Kaira specimens are uncommon in collections. According to Stowe (1986), the spiders spin small webs, hanging upside down below the web and attracting male moths that fly into a basket formed by their legs (see below). The attractant, apparently a moth pheromone, resembles that of the Bolas spiders *Mastophora*. *Mastophora* and *Kaira* both belong to the same orb-weaver family, Araneidae, but are not closely related within the family.

METHODS

This revision is one of a series for American orb weavers (Levi 1993). The procedures used are similar to those described in previous revisions (Levi 1993).

Eye measurements, as in previous papers, are expressed as ratios of the diameter (with cornea in profile) to those of the anterior median eyes (Levi 1993, figs. 27, 28). Distances between eyes of the anterior row are expressed as diameters of the anterior median eyes (in profile); distances between eyes of the posterior row are given as diameters of the posterior median eyes (in profile). The height of the clypeus, the distance between anterior median eyes and the edge of the carapace, is given in diameters of an anterior median eye and is measured below the eye (Levi 1993, fig. 28f). These measurements are approximate.

The maximum length of the abdomen was measured. In this revision "humps" refers to paired protrusions on the abdomen, and "tubercles" refers to small projections on the abdomen.

The collections used for this study came from the following institutions: (AMNH)— American Museum of Natural History, New York, United States; N. Platnick, L. Sorkin. (BMNH)—The Natural History Museum, London, England; P. Hillyard, F. Wanless. (CAS)—California Academy of Sciences, San Francisco, United States; W. J. Pulawski, D. Ubick. (MACN)—Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; E. A. Maury. (MCN)—Museu de Ciências Naturais, Fundação Zoobotąnica do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil; E. H. Buckup. (MCP)—Museu de Ciençias, Pontificia Universidade Católica, Porto Alegre, Rio Grande do Sul, Brazil; A. A. Lise. (MCZ)—Museum of Comparative Zoology, Cambridge, Massachusetts, United States. (MLP)—Museo de Universidad Nacional, La Plata, Argentina; R. F. Arrozpide. (MNHN)—Muséum National d'Histoire Naturelle, Paris, France; J. Heurtault, J. Kovoor, C. Rollard. (MNRJ)—Museu Nacional, Rio de Janeiro, Brazil; A. Timotheo da Costa. (MUSM)—Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; D. Silva D. (MZSP)—Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil; P. Vanzolini, L. Neme, J. L.

M. Leme. (USNM)—National Museum of Natural History, Smithsonian Institution, Washington, D.C., United States; J. Coddington. I thank the curators of these collections for loaning specimens. The revision of *Kaira* was started with National Science Foundation support grant no. DEB 76–115568. I thank M. Stowe for information. I am obliged to several readers, especially L. Leibensperger, L. R. Levi and E. H. Buckup for finding many errors. I thank J. C. Cokendolpher and C. D. Dondale for reviewing the manuscript and suggesting many improvements.

KAIRA SPECIES

Kaira O. P.-Cambridge

Kaira O. P.-Cambridge, 1889:56. Type species *K. gibberosa* O. P.-Cambridge, 1889, designated by F. P.-Cambridge, 1904:522.

Caira Simon, 1895:894. Changed spelling for *Kaira*, an invalid emendation.

Pronarachne Mello-Leitão, 1937:9. Type species by monotypy *P. aries* Mello-Leitão, 1937 (=*Kaira altiventer* O. P.-Cambridge). First synonymized by Levi, 1977.

Macpos Mello-Leitão, 1940:59. Type species by monotypy *M. monstrosus* Mello-Leitão, 1940 (=*Kaira gibberosa* O. P.-Cambridge). First synonymized by Levi, 1977.

Haliger Mello-Leitão, 1943:180. Type species by monotypy *H. corniferus* Mello-Leitão, 1943 (=*Kaira altiventer* O. P.-Cambridge). NEW SYNONYMY. *Note on synonymy: Haliger corniferus* is an early-instar immature described as a theridiosomatid.

Diagnosis.—*Kaira* differs from other araneids in having the abdomen attached close to the middle of its venter, rather than at its anterior end, with the axis of the abdomen almost at a right angle to the cephalothorax (Figs. 13, 56), except in *K. hiteae* (Fig. 85), *K. cobimcha* (Fig. 89), and *K. sexta*. The female has tubercles on the surface of the abdomen (Figs. 40, 55, 65, 78) or just on the anterior humps (Figs. 12, 14), except in *K. hiteae* (Fig. 85), *K. cobimcha* (Fig. 89), and *K. sexta*. The distal ends of the first to third tibiae and the metatarsi and tarsi of females are armed with many setae and macrosetae (Figs. 13, 18, 56, 60), indistinct in males. All species have dwarf males (Figs. 12, 22, 47).

Unlike other araneids, *Kaira* females have a small and lightly sclerotized epigynum, often with a flat keel-like scape (Figs. 3–5, 23–25, 48–50); the epigynum is difficult to study.

Males lack macrosetae on the palpal patella. (Males of other araneid genera have 1–3 such setae.) The median apophysis (M in Fig. 27) bears two flagella, originating from the middle of the apophysis, behind a row of teeth on its distal end (Figs. 27, 28, 41, 42), in *K. sexta* only one flagellum. The median apophysis of *K. sexta* appears turned on its long axis, having the single flagellum pointed "down" (Levi 1991, fig. 342). The distal articles of the anterior legs have only an indistinct row of setae, most of one size.

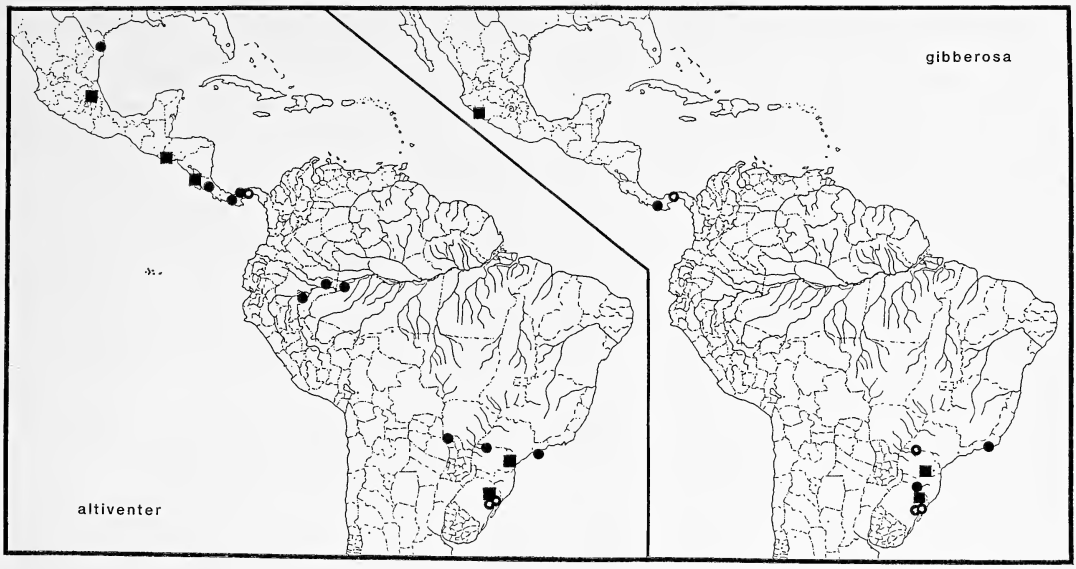
Kaira females and immatures can be confused with species of *Pozonia* (Levi, 1993). The genitalia separate *Kaira* species from species of *Ocrepeira* and *Pozonia*, which may have a similarly shaped abdomen and have setae on distal articles of the first legs, but are not closely related (judging by the structure of the genitalia).

Description.—Pale yellow-white with scattered, small, white, brown and black spots forming no distinct pattern (Figs. 12, 38, 40, 60), or transverse bands in *K. hiteae*, *K. cobimcha* and *K. sexta* (Figs. 85, 89). Carapace low, almost as wide as long, with eye region about half the width of the carapace (Figs. 1, 18, 19). Height of clypeus about equal to diameter of an anterior median eye. Eyes small and subequal in size; median ocular quadrangle usually narrower behind than in front; lateral eyes on a slight tubercle (Fig. 19). Median ocular quadrangle square or narrower behind than in front. Tibiae slightly sinuous; tarsi, metatarsi, and distal portions of tibiae armed with many setae (Figs. 13, 18, 22). Abdomen, because of its relatively posterior attachment, almost perpendicular to carapace. Abdomen differs in shape in different species, usually having tubercles, often having dorsal humps (Figs. 26, 36, 51, 60, 85).

Epigynum small, lightly sclerotized, often with median keel and posterior median plate (Figs. 3–5). Posterior median plate variable in shape in different species (Figs. 24, 49, 58, 67). Tip of keel perhaps torn by male when mating.

Shape of sternum may differ among species (not illustrated) and among individuals of same species.

Male *Kaira* less than half total length of females and with less pigment (Fig. 12). Presumably due to dwarf size, *Kaira* males lack the usual modifications of male araneids: they lack patellar macroseta, the endites are without teeth, the first coxae without hook, and second tibiae not modified. In males, the humps on the abdomen are smaller than those of females, and usually without tubercles (Figs. 22, 47). Unlike the epigynum, the palpus is well developed. Median apophysis (M in



Map 1.—Distribution of *Kaira altiventer* and *K. gibberosa*. Circles = female records, squares = male records, open circles = immature records.

Fig. 27) has two flagella and a distal row of teeth; distal hematodocha is present; embolus tip is hidden between terminal apophysis (A) and conductor (C in Figs. 27, 28). Shape of conductor separates males of *Kaira* species (C in Fig. 28).

Relationship.—The two flagella of the male median apophysis (M in Fig. 27) are believed homologous to those found in *Aculepeira*, *Amazonepeira* and *Metepeira*; the distal row of teeth on the median apophysis is also found in some species of *Metepeira*, *Aculepeira* and *Amazonepeira*. While in these genera the presence of two median apophysis flagellae in males usually correlates with a tapering, pointed scape on a lightly sclerotized (except *Aculepeira*) epigynum in females, the scape is often flattened in *Kaira*.

Natural history.—Although a *Kaira* species was known to Hentz (1850), nothing was known of their habits until recently. In response to my 1977 paper, Karl T. Stone (5 March 1978) sent his report of observations made on a *Kaira alba* female in a wide-mouth jar. The spider remained on the underside of the lid, without a web, until a fly was introduced. The spider dropped on what seemed a single thread, one-half (12 mm) inch long, and hung there until the fly blundered into her, and she clamped her legs around it, killing it.

More recently Mark Stowe (1986) reported on *Kaira alba*. They do not make an orb and specialize in catching male moths. The spider builds a small trapezoidal web, remade every 20 min, containing two triangular zigzags of threads. The spider hangs upside-down by the fourth leg on the lower and shorter parallel edge of the trapezoid spread by the other legs (Stowe 1986, fig. 5.7b). When a moth flies into the basket formed by the spider's legs, the spider drops on a short line while clasping and biting the moth. After the moth stops struggling it is wrapped in the usual araneid fashion. The wrapped moth is placed on a trapeze line between the spider's fourth legs and the hunting posture is resumed. As many as eight moths are wrapped together before the spider feeds on the package. The moths caught are listed by Stowe (1986). Since all moths caught are male, and these present only a small proportion of the available moth species, Stowe assumes that the spider uses a pheromone as an attractant. Two young observed had the same hunting posture as the adult. Although the zigzag lines are minimally viscid, they may be homologous to the viscid spiral in the araneid orb; here they play no part in food capture. The *Kaira* diurnal resting posture with legs I and II extended forward resembles that of tetragnathids. I agree with Stowe that the moth catching behavior must be independently evolved from that of *Mastophora*.

The egg sacs have an outside covering of fluffy silk and are made on top of each other (Stowe 1986, fig. 5.9). (This Stowe illustration also shows the top of the white spider, above a hanging moth.)

Matching sexes.—Immature specimens can be determined with uncertainty by the shape of the abdomen. Males have never been collected with

females. When revising the North American species (Levi 1977), I found males labeled *K. alba* by W. Gertsch and A. Archer in the collections. This appears to be correct because the male of *K. alba* has the same distribution (*e. g.*, Florida) as the female and does not fit with any other female araneid. *Kaira alba* is one of the two species whose sexes are matched with some confidence. The others are *K. hiteae* and *K. sexta*, in which the abdomen of the male is similar to that of the female.

Distribution.—*Kaira* species are known only from the Americas (Maps 1, 2). *Kaira sabino* and the male of *K. hiteae* are illustrated in Levi (1977), *K. sexta* in Levi (1991, figs. 339-342).

Misplaced species.—*Epeira electa* Keyserling, 1883, placed in *Kaira* by Levi, 1991, is probably an *Araneus*.

Kaira dromedaria O. P.-Cambridge, 1893, is a *Pozonia* (Levi 1993).

Kaira granadensis Mello-Leitão, 1941a, is a *Pozonia* (Levi 1993).

KEY TO *KAIRA* FEMALES

1. Abdomen with pair of humps, without tubercles, shield-shaped (Figs. 85, 89) 2
   Abdomen otherwise (Figs. 12, 36, 51, 78) 4
2(1). Abdomen wider than long (Fig. 89) 3
   Abdomen longer than wide (Fig. 85); south-central United States ..... *hiteae*
3(2). Epigynum in ventral view with two transverse bars (Fig. 86); southern Brazil (Map 2) .... *cobimcha*
   Epigynum in ventral view with only corners of anterior bar showing (Levi 1991, fig. 339); Guatemala to Amazon area (Map 2) ..... *sexta*
4(1). Epigynum with a median notch in a posterior transverse bar (Levi 1977, fig. 141); Arizona (Map 2) ..... *sabino*
   Epigynum otherwise; not in Arizona 5
5(4). Abdomen with a long median anterodorsal projection (Figs. 69, 73, 74) 6
   Abdomen with a pair or more of humps or slight median projections (Figs. 12, 36, 60) 7
6(5). Abdomen drop-shaped (Fig. 69); northern Argentina (Map 2) ..... *candidissima*
   Abdomen a long cone (Figs. 73, 74); southeastern Brazil to northern Argentina (Map 2) ..... *conica*
7(5). Posterior of abdomen without tubercles (Figs. 12–18, 26, rarely one pair of small humps, Levi 1977, fig. 134) 8
   Posterior of abdomen with humps or tubercles (Figs. 40, 51, 65, 78) 9
8(7). Epigynum with longitudinal projection (Figs. 23–25); southeastern United States to northern Mexico (Map 2) ..... *alba*
   Epigynum with transverse projection (Figs. 3–11); Texas to southern Brazil (Map 1) ..... *altiventer*
9(7). Abdomen much longer (or higher) than wide (Fig. 35) 10
   Abdomen as wide or wider than long (Figs. 65, 78) 11
10(9). Abdomen rounded anteriorly (Fig. 51); Colombia (Map 2) ..... *tulua*
   Abdomen with a pair of dorsal humps (Figs. 35–40); Mexico to southern Brazil (Map 1) ... *gibberosa*
11(9). Abdomen rectangular (Figs. 55, 78) 12
   Abdomen subcircular (Figs. 60, 65); Peruvian Amazon region 13
12(11). Epigynum with extended scape (Fig. 75–77); southeastern Brazil (Map 2) ..... *echinus*
   Epigynum with a short scape (Figs. 52–54); Peruvian Amazon region (Map 2) ..... *erwini*
13(11). Epigynum as in Figures 61–64; Map 2 ..... *dianae*
   Epigynum as in Figures 57–59; Map 2 ..... *shinquito*

KEY TO *KAIRA* MALES

(Males of *K. candidissima*, *K. conica*, *K. dianae*, *K. erwini*, *K. sabino*, *K. shinguito*, *K. tulua* are unknown.)

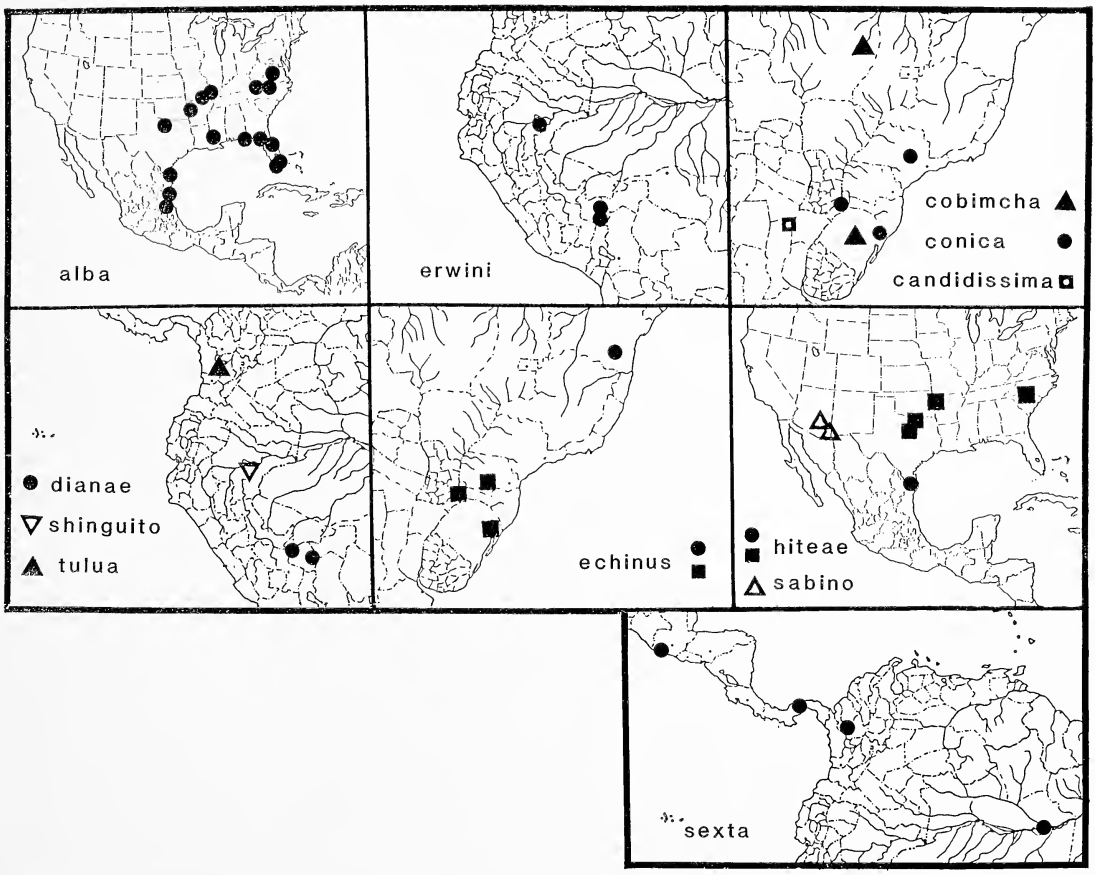
1. Median apophysis twisted, with only one flagellum (Levi 1991, fig. 342); Guatemala to Amazon area (Map 2) ..... *sexta*
   Median apophysis not twisted, with two flagella (Figs. 20, 21, 79, 80, 90, 91) 2
2(1). Abdomen wider than long (Fig. 81); conductor of palpus as in Figure 80; from Bahia State, Brazil to northern Argentina (Map 2) ..... *echinus*
   Abdomen longer than wide (Figs. 22, 47, 92); conductor of palpus otherwise 3

3(2). Abdomen dorsum with an anterior dorsal shield (Fig. 92); terminal apophysis with "transverse" sclerotized edge (Fig. 91); Mato Grosso, Brazil (Map 2) ..... *cobimcha*
Abdomen without dorsal shield (Figs. 22, 47) 4
4(3). Conductor with a distal tooth on side of terminal apophysis (Figs. 42, 44, 46); Mexico to southern Brazil (Map 1) ..... *gibberosa*
Conductor without distal tooth on conductor (Figs. 21, C in 28) 5
5(4). Median apophysis of palpus with only 3 or 4 large teeth (Figs. 20, 21); Texas to southern Brazil (Map 1) ..... *altiventer*
Median apophysis with more than 6 teeth (M in Figs. 27, 28) 6
6(5). Conductor with dark distal swelling overhanging subdivided lateral pockets (Levi 1977, fig. 140); terminal apophysis bluntly pointed (Levi 1977, fig. 139); south-central United States (Map 2) ... *hiteae*
Tip of conductor facing flagella (C in Fig. 28); terminal apophysis sharply pointed (A in Fig. 27); southeastern United States to northern Mexico (Map 2) ..... *alba*

Kaira altiventer O. P.-Cambridge
Figures 3–22; Map 1

Kaira altiventer O. P.-Cambridge, 1889:56, pl. 3, fig. 13, ♀. Female holotype from Veragua [Veraguas Prov.], Panama, in BMNH, examined. Keyserling, 1892: 62, pl. 3, fig. 48, ♀. F. P.-Cambridge, 1904: 522, pl. 51, fig. 10, ♀ Levi, 1977:218, figs. 130–137, ♀, ♂.

? *Caira spinosa* Simon, 1897:478. Female lectotype designated by Levi, 1977 and imm. paralectotype from São Paulo de Olivença, Amazonas State, Brazil, and Pebas, Depto. Loreto, Peru in MNHN, examined. First synonymized by Levi, 1977.



Map 2.—Distribution of *Kaira* species. Circles of *K. echinus* and *K. hiteae* = female records, squares = male records.

? *Caira capra* Simon, 1897:479. Immature holotype from Paraguay in the MNHN, examined. NEW DOUBTFUL SYNONYMY.

Pronarachne aries Mello-Leitão, 1937:9, fig. 10, ♀. Female holotype from Itatiaia, Rio Grande do Sul in MNRJ, examined. First synonymized by Levi, 1977.

Haliger corniferus Mello-Leitão, 1943:180, fig. 18, imm. Immature holotype from Rio Grande do Sul in MNRJ, lost. Brignoli, 1983:239. NEW SYNONYMY.

Synonymy.—The holotype of *Caira spinosa* is a large, mature individual, 13.5 mm total length, abdomen 10.3 mm high, with only one pair of tubercular humps and tubercles between (Figs. 14, 15). The *Caira capra* holotype is immature (5.8 mm total length) and lacks some of the tubercles on the humps of the abdomen (Fig. 18). The holotype of *Pronarachne aries* has a flat triangular scape (Figs. 9–11) as in *K. altiventer* but the abdominal humps are much thinner than in other females (Figs. 16, 17, 19). The holotype of *Haliger coniferus*, originally placed in Theridiosomatidae, is only 2.5 mm total length, lacks tubercles on the humps and on the posterior of the abdomen, and has a thin white line going from the tip of one hump to the tip of the other, as do other specimens from this area (Fig. 12). Coddington (1986), in his study of theridiosomatids, considered *Haliger* unrecognizable, but it had been misplaced in that family. None of these specimens has posterior tubercles on the abdomen.

Description.—*Female from Paraná State, Brazil:* Carapace yellowish, cephalic region with tiny, irregular black spots. Chelicerae, labium, endites spotted orange. Sternum orange with brown line all around. Coxae orange, with dark brown spots; legs orange with tiny black spots. Dorsum of abdomen with posterior part darker than anterior and with minute stipples, a light transverse line between humps (Fig. 12), and larger black spots on tubercles; sides and venter spotted. Eyes subequal in size. Anterior median eyes 1.5 diameters apart. Posterior median eyes 1.2 diameters apart. Height of clypeus equals 1.4 diameters of the anterior median eyes. Sternum elongate, extending between fourth coxae. Abdomen with two humps, bearing asymetrical tubercles (Figs. 12, 13). Total length 10 mm. Carapace 4.2 mm long, 3.8 wide, behind lateral eyes 1.8 wide. First femur 5.4 mm, patella and tibia 6.7, metatarsus 3.3, tarsus 1.2. Second patella and tibia 5.4 mm, third 2.9, fourth 3.5. Abdomen 9.4 mm high.

Male from Hidalgo, Mexico: Color as in female but legs with wide, dark rings, and sides of the abdomen with irregular dusky spots having a colorless center (Fig. 22). Posterior median eyes 1.2 diameters of anterior medians, laterals 1 diameter. Anterior median eyes 1.2 diameters apart, 1 diameter from laterals. Posterior median eyes their diameter apart, 2.1 diameters from laterals. Height of clypeus equals 0.9 diameter of the anterior median eyes. Abdomen with a pair of anterior humps (Fig. 22). Total length 2.0 mm. Carapace 1.00 mm long, 0.84 wide, behind lateral eyes 0.53 wide. First femur 1.06 mm, patella and tibia 1.30, metatarsus 0.71, tarsus 0.47. Second patella and tibia 1.00 mm, third 0.58, fourth 0.76. Abdomen 1.58 mm high.

Note: Males and females have not been collected together but were matched by Levi, 1977, because they have physical similarities and were collected in Mexico and Central America.

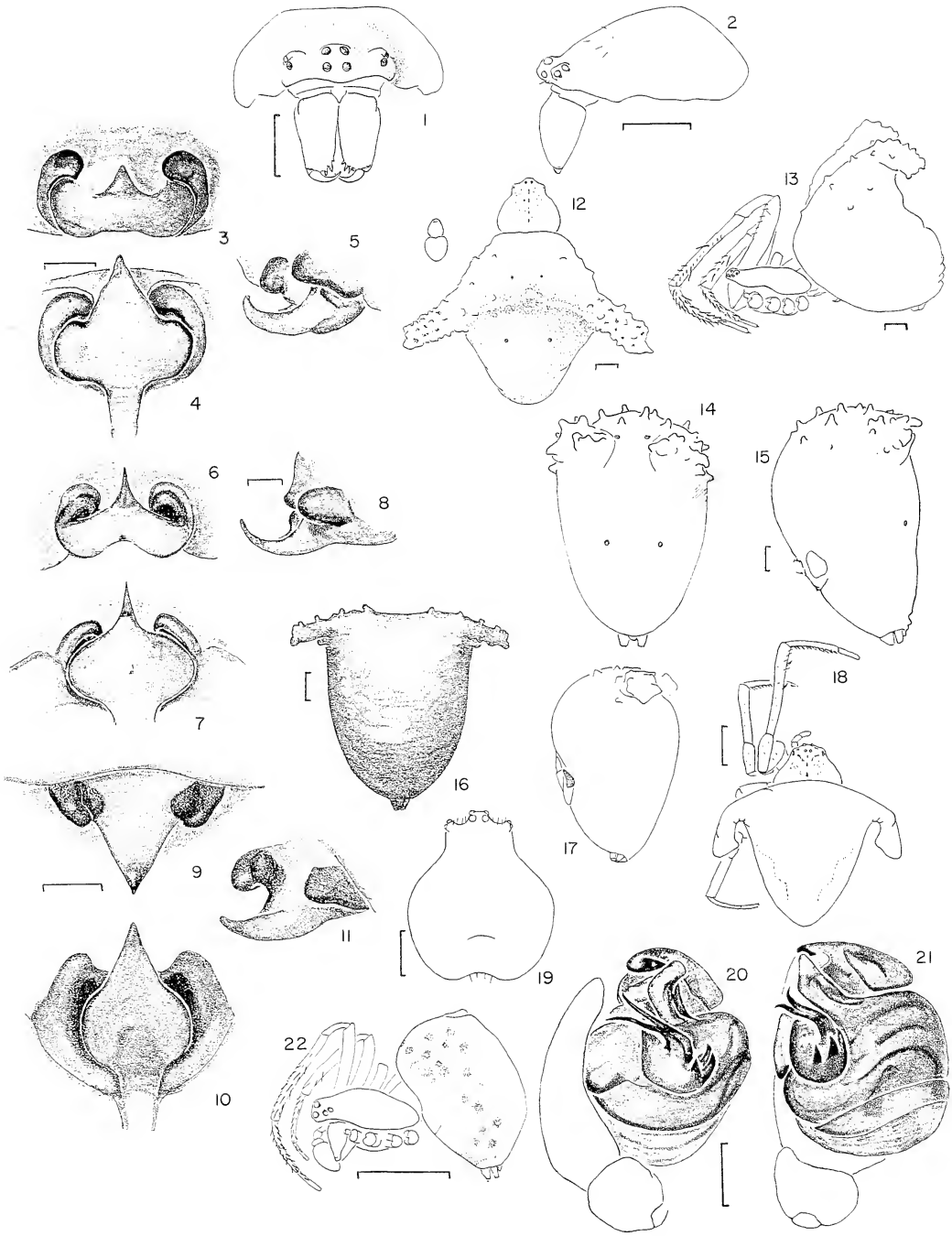
Variation: Total length of females 7.0 to 13.5 mm, males 1.9 to 2.2. Illustrations (Figs. 3–5, 12, 13) were made from a female from Paraná State, Brazil and a male (Figs. 20–22) from Hidalgo State, Mexico. Some females have the humps curved, with their tips approaching and almost touching, forming an "O". The illustration (Levi 1977) fig. 134, was made of a female from Edinburg, Texas; unlike all others, it had a pair of posterior tubercles. The immature holotypes of *C. capra*, *H. corniferus* and the immature specimen from Montenegro, Rio Grande do Sul, all lack tubercles on the humps of the abdomen (Fig. 18).

Diagnosis.—The epigynum of the female, unlike that of *K. alba*, has a flat, triangular, curved scape, the tip projecting anteriorly (Figs. 3, 6) and, like *K. alba* but unlike others, no humps or tubercles on the posterior of the abdomen (Figs. 12–18). The tiny male can be separated from others by having a palpus with only three or four long, black teeth on the distal end of the median apophysis and by the shape of the conductor, pointed and longest on the side of the dark terminal apophysis (center and 1100 h of Fig. 21).

Natural History.—A male from Texas was collected in low shrubs; another was the prey of a *Trypargilum nitidum* wasp in Costa Rica. One female in Peru was found hanging on a thread, another was obtained at the same location by fogging the canopy.

Distribution.—Southern Texas to southern Brazil (Map 1).

Additional specimens examined.—MEXICO. *Hidalgo:* El Salto, 22–23 April 1967, ♂ (W. Peck, CAS).



Figures 1–22.—*Kaira* species: *K. alba* carapace and chelicerae (1, 2); 1, frontal; 2, lateral. *K. altiventer* (3–22); 3–17, 19, female; 3–11, epigynum; 3, 6, ventral; 9, anterior; 4, 7, 10, posterior; 5, 8, 11, lateral; 12, dorsal with small male, same scale; 13, 15, 17, lateral; 14, 16, posterior; 19, carapace; 20–22, male; 20, 21, left palpus; 20, mesal; 21, ventral; 22, lateral; 3–5, 12, 13, from Paraná State, Brazil; 6–8, 14, 15, holotype of *Caira spinosa*; 9–11, 16, 17, 19, holotype of *Pronarachne aries*; 18, immature holotype of *Caira capra*; 20–22, from Hidalgo State, Mexico. Scale lines = 1.0 mm, of genitalia = 0.1 mm.

EL SALVADOR. *San Salvador:* January, March 1954, ♂ (J. B. Boursol, AMNH). **COSTA RICA**. *San José:* San Antonio de Escazu, 1400 m, 9 October 1982, ♀ (W. Eberhard SAI-73, MCZ), November 1988, ♀ (W. Eberhard, USNM). **PERU**. *Loreto:* Río Samiria, 29 May 1990, ♀ (D. Silva D, MUSM), 20 May 1990, imm. (T. Erwin, D. Silva D, MUSM). **BRAZIL**. *São Paulo:* Ilha São Sebastião, 28 Jan. 1951, ♀ (MZSP 6608). *Paraná:* Rôlandia, 1948, ♀ (A. Maller, AMNH); Almirante Tamandaré, 8 Aug. 1984, ♂ (C. C. Costa, MCN 12,500). *Rio Grande do Sul:* Montenegro, 1 September 1979, imm. (H. Bischoff, MCN 6431); Ponta Grossa, Porto Alegre, 7 May 1976, imm. (A. A. Lise, MCN 4241); Triunfo, 15 September 1977, imm. (A. A. Lise, MCN 6492); Viamão, 22 October 1988, ♂ (A. B. Bonaldo, MCN 17953). **PARAGUAY**. *Concepción:* Apa, Aug. 1909, ♀ (AMNH).

Kaira alba (Hentz)
Figures 1, 2, 23–28; Map 2

Epeira alba Hentz, 1850:20, pl. 3, fig. 7. Female from North Carolina, destroyed.
Kaira alba: - Levi, 1977:216, figs. 117-129, ♀, ♂. Stowe, 1986: 115, fig. 5, 7 (web).

Description.—*Female from Virginia:* Cephalothorax yellow-white with brown spots and streaks; sternum spotted, legs with rings and spots. Abdomen white with a dark patch between humps; venter dusky, spotted. Eyes subequal in size. Anterior median eyes 1.3 diameters apart, 1.4 diameters from laterals. Posterior median eyes 1 diameter apart, 1.5 diameters from laterals. Height of clypeus equals 0.7 diameter of anterior median eye. Abdomen with a pair of dorsal humps with tubercles (Fig. 26). Total length 4.8 mm. Carapace 2.1 mm long, 1.8 wide, behind lateral eyes 0.9 wide. First femur 2.5 mm, patella and tibia 3.1, metatarsus 1.7, tarsus 0.7. Second patella and tibia 2.3 mm, third 1.2, fourth 1.8. Abdomen 4.1 mm high.

Male from North Carolina: Carapace yellowish, with eye area dusky, with a median dusky band, and with thoracic region having dusky margin. Chelicerae yellowish with dusky patch. Sternum with black marks. Legs with dusky rings and spots. Dorsum of abdomen white with a black patch between humps and scattered black spots of various sizes; venter dusky. Posterior median eyes 1.2 diameters of anterior medians, laterals 1 diameter. Anterior median eyes their diameter apart, their diameter from laterals. Posterior median eyes 0.5 diameter apart, 1 diameter from laterals. Height of clypeus equals 0.8 diameter of anterior median eye. Abdomen widest in middle, humps slightly tubercular. Total length 2.6 mm. Carapace 1.38 mm long, 1.11 wide, 0.65 wide behind lateral eyes. First femur 1.61 mm, patella and tibia 1.96, metatarsus 1.47, tarsus 0.36. Second patella and tibia 1.54 mm, third 0.87, fourth 1.01. Abdomen 1.87 mm high.

Note: Males and females were matched because of similarly shaped abdomens and because both were collected in the same areas of the United States (Map 2).

Variation: Total length of females 4.8–7.2 mm, males 2.6–2.9. Female abdomens 4.1–8.2 mm high. Illustrations were made from a female from Virginia and a male from North Carolina.

Diagnosis.—As in *K. altiventer*, females of *K. alba* lack posterior humps or tubercles on the abdomen (Fig. 26) but differ by the vertical keel of the epigynum (Figs. 23–25). The median apophysis of the male palpus differs from that of *K. alba* in having six or more teeth (Figs. 27, 28), and the conductor differs from that of *K. altiventer* in being longest on the side closest to the median apophysis (C in Fig. 28).

Natural History.—Observations are given in the introduction to the genus.

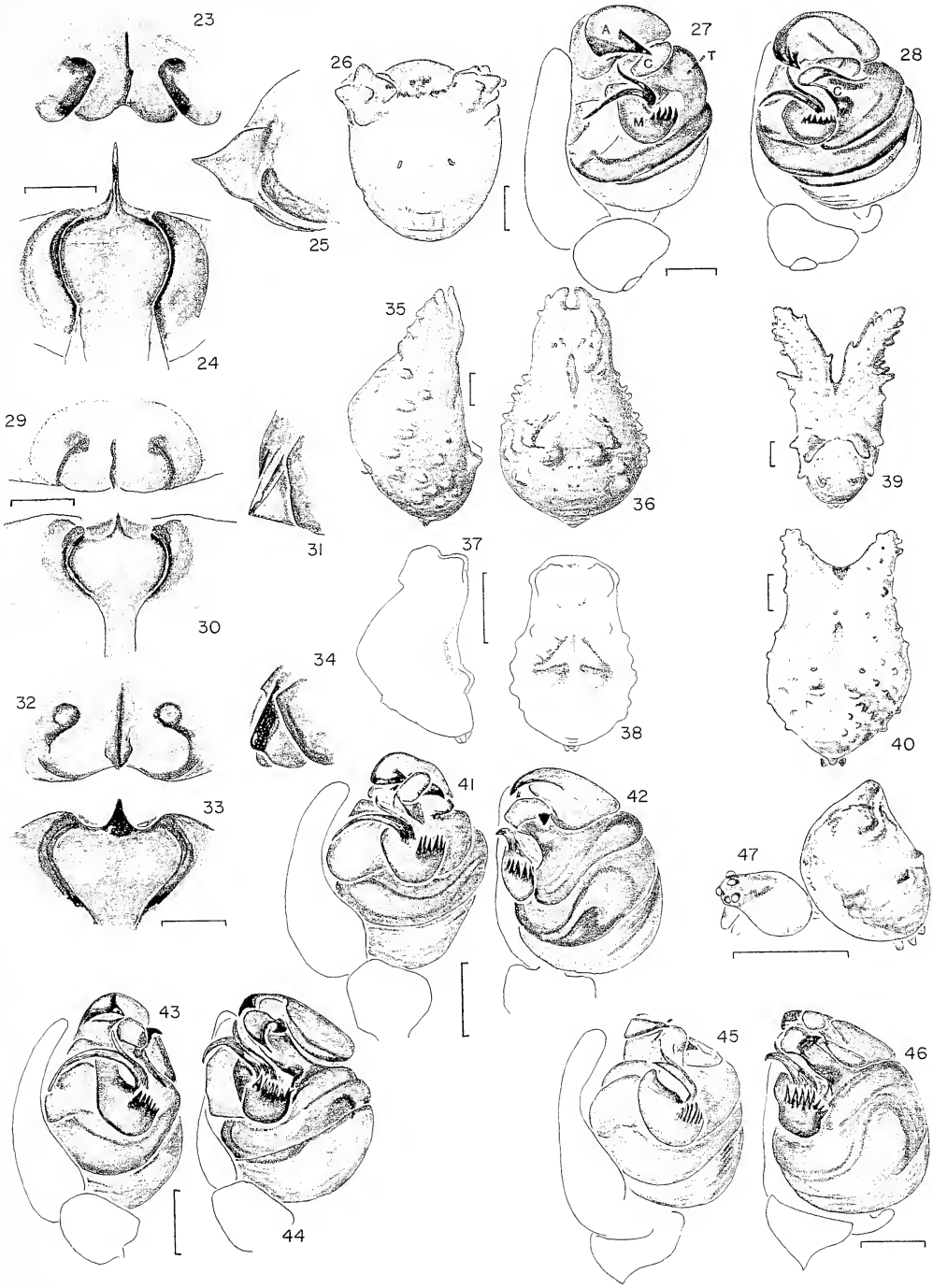
Distribution.—Virginia to Mexico (Map 2).

Additional specimen examined.—UNITED STATES. *Virginia:* Black Pond [?], 14 Sept. 1913, ♀ (USNM).

Kaira gibberosa O. P.-Cambridge
Figures 29-47; Map 1

Kaira gibberosa O. P.-Cambridge, 1890:57, pl. 3, fig. 12, ♀. Female holotype from Veragua [Veraguas Prov.;], Panama, in BMNH, examined. Keyserling, 1892:63, pl. 3, fig. 49, ♀. F. O. P.-Cambridge, 1904: 522, pl. 51, fig. 9, ♀. Roewer, 1942: 904.
Kaira obtusa Keyserling, 1892:66, pl.3, fig. 51, imm. Immature holotype from Taquara, Rio Grande do Sul, in BMNH, examined. Roewer, 1942:904. NEW SYNONYMY.
? *Macpos monstrosus* Mello-Leitão, 1940:59, fig. 6, ♀. Female holotype from Jardim Botânico, Rio de Janeiro, Brazil in MNRJ, lost. DOUBTFUL NEW SYNONYMY.
Wagneriana minutissima Mello-Leitão, 1941b:250. Male holotype from Rio Negro, Paraná State, Brazil, in MNRJ, no. 58298, examined. Brignoli, 1983:281. NEW SYNONYMY.
Caira gibberosa: - Bonnet, 1956:925.
Caira obtusa: - Bonnet, 1956:925.
Kaira monstrosa: - Brignoli, 1983:271.

Note: The type locality of *K. gibberosa* is Veragua, Panama. Veragua refers to Veraguas Prov-



Figures 23–47.—*Kaira* species: *K. alba* (23–28); 23–26, female; 23–25, epigynum; 23, ventral; 24, posterior; 25, lateral; 26, abdomen, dorsal; 27, 28, left male palpus; 27, mesal; 28, ventral. *K. gibberosa* (29–47); 29–36, 39, female; 29–34, epigynum; 29, 32, ventral; 30, 33, posterior; 31, 34, lateral; 35, 36, 39, abdomen; 37, 38, 40, immature abdomen; 35, 37, lateral; 36, 38–40, posterior; 41–47, male; 41–46, palpus; 41, 43, 45, mesal; 42, 44, 46, ventral; 47, dorsolateral; 29–31, 35, 36, holotype of *K. gibberosa*; 39, holotype of *Macpos monstrosus* (after Mello-Leitão); 37, 38, immature holotype of *K. obtusa*; 40, penultimate female from Paraná State, Brazil; 45, 46, holotype of *K. minutissima*; 41, 42, from Michoacan State, Mexico; 43, 44, from Rio Grande do Sul State, Brazil. Abbreviations: A, terminal apophysis; C, conductor; M, median apophysis; T, tegulum. Scale lines = 1.0 mm, of genitalia = 0.1 mm.

ince, Panama (Selander & Vaurie, 1962). The fragmented holotype has insect-pin holes. It is larger (total length 6.0 mm, abdomen 7. 0 mm high) than the specimen from Paranáa State, Brazil, but the measurements of the carapace and legs are similar.

The holotype of *Kaira obtusa*, although immature, has anterior and posterior humps on the abdomen (Figs. 37, 38), as does *K. gibberosa*. This species seems relatively common in southern Brazil, the type locality of *K. obtusa*. The specimen has a total length of 3.0 mm. Carapace 1.40 mm long, 1.35 wide, behind lateral eyes 0.70 wide. First femur 1.59 mm, patella and tibia 1.95, metatarsus 1.01, tarsus 0.48. Second patella and tibia 1.49 mm, third 0.87, fourth 1.09. Abdomen (shrivelled) 3.0 mm high. The name *Kaira obtusa* was erroneously synonymized with *K. altiventer* by Levi, 1977.

The holotype of *Macpos monstrosus* has a total length of 6 mm, the first patella and tibia 5.5 mm (measurements from Mello-Leitõ 1940) almost twice the length of the female of *K. gibberosa* illustrated. Mello-Leitão's illustration of the female from the side and the abdomen from posterior (Fig. 39) suggest that it may be this species, but the abdomen does not narrow dorsally and the anterior humps are almost as long as the abdomen below (Fig. 39).

According to Mello-Leitão (1941b), *Wagneriana minutissima* is described from a female, but the holotype and description are of a male. The holotype resembles the male illustrated (Figs. 45, 46) but is poorly preserved and the median apophysis flagellae of the left palpus are broken off.

Description.—*Female from Paraná State, Brazil:* The animal is heavily pigmented with brown spots, some black and white streaks, cephalic region darkest. Sternum dusky orange. Legs spotted and streaked, distal ends of femora and patellae dark brownish black with white streaks. Dorsum of abdomen dark between humps and posteriorly with a black chevron pointing anteriorly (Figs. 35, 36). Eyes subequal in size. Anterior median eyes 1.3 diameters apart, 1.8 diameters from laterals. Posterior median eyes 1.2 diameters apart, 2.5 diameters from laterals. Height of clypeus 0.7 diameter of anterior median eye. Abdomen with two pairs of humps and tubercles on sides of abdomen (Fig. 35–40). Total length 5.2 mm. Carapace 2.5 mm long, 2.1 wide, behind lateral eyes 1.2 wide. First femur 2.8 mm, patella and tibia 3.6, metatarsus 1.7, tarsus 0.7. Second patella and tibia 2.6 mm, third 1.5, fourth 2.1. Abdomen (shrivelled) 4.6 mm high.

Male from Vacaria, Rio Grande do Sul State: Carapace pale yellowish white with white streaks, a dusky patch covering cephalic region (Fig. 47). Sternum pale light yellowish, appearing spotted. Legs pale yellowish with distal halves of femora and patellae dark dusky. Abdomen with white line behind and around anterior protrusions, darker patches on paired posterior swellings with white mark behind; sides darker; venter pale (Fig. 47). Eyes subequal in size. Anterior median eyes 0.8 diameter apart, 0.7 diameter from laterals. Posterior median eyes 0.9 diameter apart, 1.5 diameters from laterals. Height of clypeus equal to 0.5 diameter of anterior median eye. Abdomen with a pair of diagonal, dorsal humps and pair of smaller posterior humps (Fig. 47). Total length 2.0 mm. Carapace 0.91 mm long, 0.83 wide, behind lateral eyes 0.47 wide. First femur 0.88 mm, patella and tibia 1.53, metatarsus 0.58, tarsus 0.41. Second patella and tibia 0.87 mm, third 0.52, fourth 0.69. Abdomen 1.46 mm high.

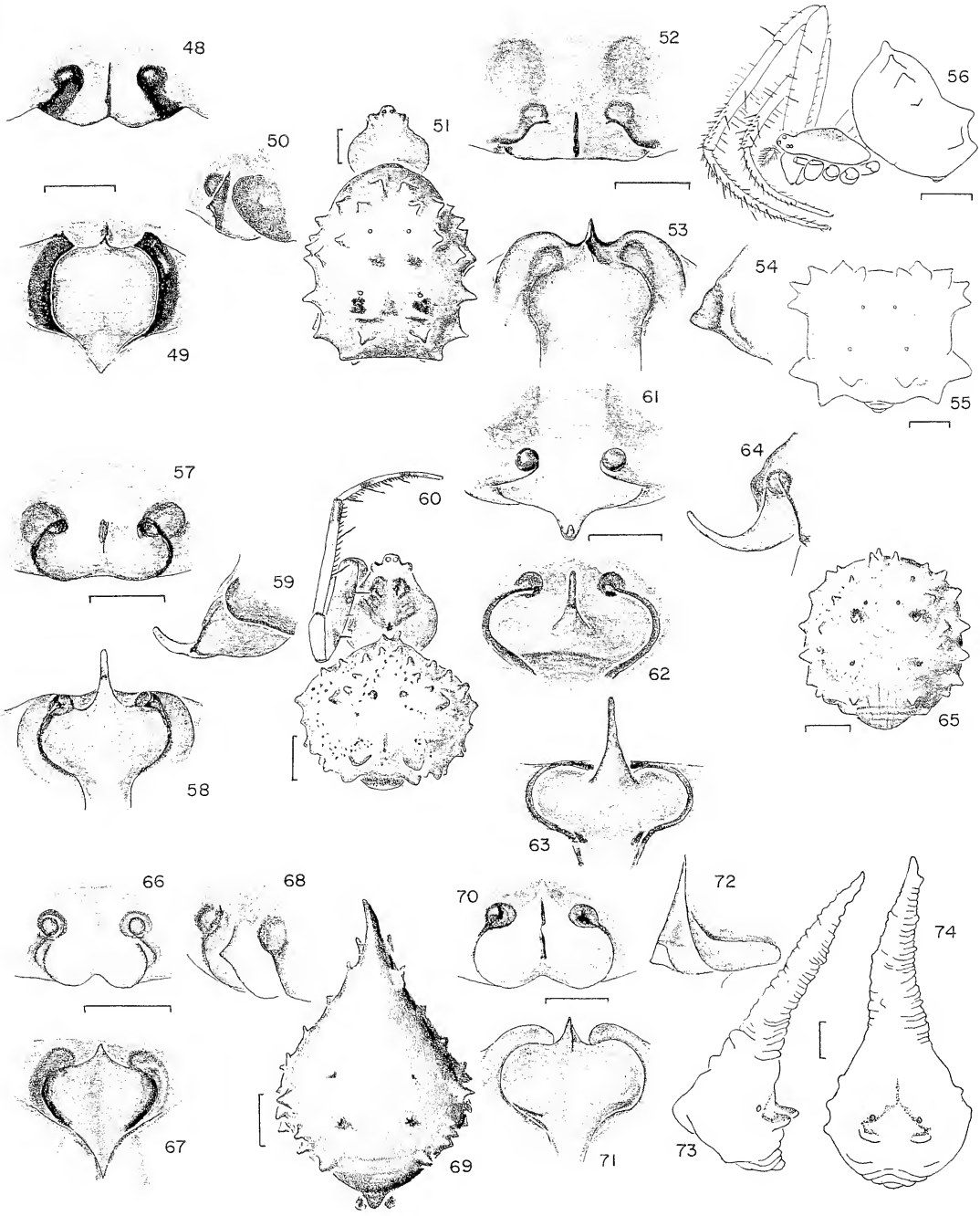
Note: Males and females were matched because they were collected in the same area and both have a posterior pair of humps on the abdomen (Figs. 35–40, 47).

Variation: Total length of females 5.2 to 8.0 mm, abdomen 4.6 to 8.0 mm high. Illustrations were made from a female from Paraná State and male from Vacaria, Rio Grande do Sul. In the male from Michoacan State, Mexico, the conductor of the palpus (Fig. 42) is shorter than in males from southern Brazil (Figs. 43–46). I assume they belong to one species.

Diagnosis.—The female differs from other species of *Kaira* by having a longitudinal, keel-shaped scape in the epigynum (Figs. 23–25, 29–34) and by having a second pair of dorsal tuberculate humps on the abdomen, and tubercles on the posterior humps and on the sides (Figs. 35–40). The male is separated from others by having a distal black tooth on the conductor of the palpus (Figs. 41–46).

Distribution.—Mexico to southern Brazil (Map 1).

Specimens examined.—**MEXICO**. *Michoacan:* 78 km SE Aquila, 13 July 1984, ♂, doubtful determ. (J. B. Woolley, MCZ.). **PANAMA**. *Panamá:* Summit, Aug. 1950, 2 imm., 19 Aug. 1954, imm. (A. M. Chickering, MCZ). **BRAZIL**. *Paraná:* Rolândia, May 1947, 2 penult. ♀, 1948, ♀ (A. Maller, AMNH). *Santa Catarina:*



Figures 48–74.—*Kaira* species: ***K. tulua***, female (48–51); 48–50, epigynum; 48, ventral; 49, posterior; 50, lateral; 51, dorsal. ***K. erwini***, female (52–56); 52–54, epigynum; 52, ventral; 53, posterior; 54, lateral; 55, abdomen, posterior; 56, lateral. ***K. shinguito***, female (57–60); 57–59, epigynum; 57, ventral; 58, posterior; 59, lateral; 60, dorsal. ***K. dianae***, female (61–65); 61–64, epigynum; 61, anterior; 62, ventral; 63, posterior; 64, lateral; 65, abdomen, posterior. *K. candidissima*, female (66–69); 66–68, epigynum; 66, ventral; 67, posterior; 68, lateral; 69, abdomen, posterior. *K. conica*, female (70–74); 70–72, epigynum; 70, ventral; 71, posterior; 72, lateral; 73, 74, abdomen; 73, lateral; 74, posterior. Scale lines = 1.0 mm, of genitalia = 0.1 mm.

Pinhal, 700 m, May 1947, 2 penult. ♀ (A. Maller, AMNH). *Rio Grande do Sul:* Vacaria, 21–25 Apr. 1982, ♂ (A. A. Lise, MCN 10295); Porto Alegre, Morro Santana, 1 Sept. 1984, imm. (A. A. Lise, MCN).

Kaira tulua new species
Figures 48–51; Map 2

Holotype.—Female holotype from Río Tuluá, 1100 m, Depto. Valle, Colombia, Aug. 1977 (W. Eberhard E–231), in MCZ. The specific name is a noun in apposition after the locality.

Description.—Female holotype. Carapace pale yellow-white with white spots. Chelicerae, labium, endites and sternum yellow-white. Legs pale yellow-white with a black spot on the anterior face of tibiae and tarsi. Dorsum of abdomen whitish with a pair of posterior black marks (Fig. 51); venter whitish. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.8 diameter. Anterior median eyes 1.1 diameters apart, 1.8 diameters from laterals. Posterior median eyes 1.1 diameters apart, 2.8 diameters from laterals. Lateral eye tubercles distinct. Height of clypeus equals 0.8 diameter of anterior median eye. Abdomen without large protrusions, but covered with tubercles that are not symmetrical (Fig. 51). Total length 7.0 mm. Carapace 2.9 mm long, 2.7 wide, 1.2 behind lateral eyes. First femur 2.8 mm, patella and tibia 3.9, metatarsus 2.1, tarsus 1.0. Second patella and tibia 3.0 mm, third 1.8, fourth 2.5. Abdomen 5.8 mm high.

Diagnosis.—The round anterior profile of the abdomen, posteriorly truncate, and covered with tubercles (Fig. 51) distinguishes this species. The epigynum has a small keel with a posterior median plate as wide as long (Figs. 48–50).

Kaira erwini new species
Fig. 52–56; Map 2

Holotype.—Female holotype from Río Samiria, Cocha Shinguito, Depto. Loreto, Peru, June 1990 (T. Erwin), in MUSM. The species is named after the collector, the entomologist T. Erwin.

Description.—*Female holotype:* Cephalothorax pale yellowish white with a brown stippled patch on the carapace and a brown spot on the posterior of second tibia. Dorsum of abdomen with white pigment spots; white pigment on venter and underside of tubercles. Eyes subequal in size. Anterior median eyes their diameter apart, 1.4 diameters from laterals. Posterior median eyes 0.8 diameter apart, 1.8 diameters from laterals. Height of clypeus equals diameter of anterior median eye. Abdomen wider than long, with five pairs of small humps anteriorly, three pairs posteriorly (Figs. 55, 56). Total length 4.3 mm. Carapace 2.1 mm long, 2.1 wide, 0.9 behind lateral eyes. First femur 3.1 mm, patella and tibia 3.6, metatarsus 2.2, tarsus 1.1. Second patella and tibia 2.5 mm, third 1.5, fourth 2.1. Abdomen 3.1 mm high.

Variation: Total length of females 4.0–5.0 mm.

Diagnosis.—*Kaira erwini* differs from *Kaira echinus* by the placement of the humps on the abdomen (Figs. 55, 56) and by having a long, keel-shaped, pointed scape on the epigynum (Figs. 52–54).

Specimens examined.—**PERU**. *Loreto:* Río Samiria, fogging, 20 May 1990, ♀ paratype (T. Erwin, D. Silva, MUSM). *Madre de Dios:* Tambopata, trocha del bamboo, 290 m, 7 June 1988, ♀ (D. Silva, MUSM); Albergue Cuzco Amazonica, 12°33′S, 69°03′W, 6 Mar. 1990, night coll., ♀ (D. Silva, MCZ).

Kaira shinguito new species
Figs. 57-60; Map 2

Holotype.—Female holotype from Río Samiria, Cocha Shinguito [ox-bow lake], Depto. Loreta, Peru, 22 May 1990 (D. Silva D.), in MUSM. The specific name is a noun in apposition after the locality.

Description.—*Female holotype:* Carapace pale yellow-white, with a pair of brown patches containing darker veins surrounded by some white pigment spots, and a dark spot posteriorly. Chelicerae yellow-white with brown patches. Labium, endites yellow-white. Sternum brown. Coxae yellow-white with brown spot; legs yellow-white. Dorsum of abdomen yellow-white with some scattered small brown dots (Fig. 60); venter with five indistinctly separated brown bands between epigynum and spinnerets. Eyes subequal. Anterior median eyes 0.9 diameter apart, 1.2 diameters from laterals. Posterior median eyes 0.8 diameter apart, 2 diameters from laterals. Height of clypeus equals 0.6 diameter of anterior median eye. Abdomen subspherical with paired tubercles (Fig. 60). Total length 5.1 mm. Carapace 2.2 mm long, 2.1 wide, 1.1 behind lateral eyes. First femur 3.1 mm, patella and tibia 3.4, metatarsus 2.4, tarsus 1.1. Second patella and tibia 2.7 mm, third 1.6, fourth 2.0. Abdomen 3.7 mm high.

Diagnosis.—This female differs from those of other species by the shape of the abdomen (Fig. 60) and by the shape of the scape of the epigynum (Figs. 57–59).

Kaira dianae new species
Figs. 61–65; Map 2

Holotype.—Female holotype from Zona Reservada Pakitza, on low leaf of tree, 356 m, Depto. Madre de Dios, 11°56′S, 71°17′W, Peru, 27 Sept. 1991 (D. Silva D.) in MUSM. The species is named after the collector.

Description.—*Female holotype:* Carapace pale yellowish white with brown and black speckles in cephalic region, eye region with white pigment, thoracic region with black border on sides. Chelicerae, labium, endites yellowish white. Sternum brown-black. Coxae, legs pale yellowish white with brown and black speckles and some white pigment. Dorsum of abdomen yellowish white, speckled with black and tiny white spots; a pair of black patches on anterior dorsal tubercles (Fig. 65); venter speckled. Eyes subequal in size. Anterior median eyes 0.8 diameter apart, 1.1 diameters from laterals. Posterior median eyes 0.6 diameter apart, 1.9 diameters from laterals. Height of clypeus equals 0.8 diameter of anterior median eye. Abdomen almost spherical, slightly longer than wide with tubercles, none quite symmetrical (Fig. 65). Total length 5.5 mm. Carapace 2.4 mm long, 2.3 wide, 1.1 behind lateral eyes. First femur 3.1 mm, patella and tibia 3.8, metatarsus 2.3, tarsus 1.1. Second patella and tibia 2.8 mm, third 1.7, fourth 2.2. Abdomen 4.2 mm high.

Variation: The immatures (of uncertain determination) have the sternum with light areas.

Diagnosis.—*Kaira dianae* differs from *K. shinquito* by having a curved tubular scape on the epigynum (Figs. 61–64) and from other species by the subspherical, tuberculate abdomen (Fig. 65).

Specimens examined.—**PERU**. *Madre de Dios:* 15 km E Puerto Maldonado, 12°33′S, 69°03′W, 23–25 June 1989, 2 imm. (D. Silva D., MUSM).

Kaira candidissima (Mello-Leitão)
Figs. 66–69; Map 2

Macpos candidissimus Mello-Leitão, 1941c:212, figs. 18, 19, ♀. Female holotype from El Rabón, Santa Fé Province, Argentina, in MLP, no. 15135, examined.
Kaira candidissima: - Brignoli, 1983:271.

Description.—*Female holotype:* Carapace, sternum, legs pale yellow-white. Dorsum of abdomen white with sides and venter pale yellow-white. Eyes subequal in size, very small. Anterior median eyes slightly less than two diameters apart. Posterior median eyes slightly more than one diameter apart. Height of clypeus equals slightly more than one diameter of anterior median eye. Abdomen tapers dorsally to a single point (Fig. 69). Total length 6 mm. Carapace 2.6 mm long, 2.1 wide, behind lateral eyes 1.0 wide. First femur 2.6 mm, patella and tibia 3.3, metatarsus 1.7, tarsus 1.4. Second patella and tibia 2.7 mm, third 1.7, fourth 2.0. Abdomen 6.2 mm high.

Diagnosis.—The female differs from *K. conica* by having smaller eyes, a drop-shaped abdomen (Fig. 69) and the sternum widest between second and third coxa.

Kaira conica Gerschman & Schiapelli
Figs. 70–74; Map 2

Kaira conica Gerschman & Schiapelli, 1948:11, fig. 11–13, ♀. Female holotype from Santa María, Misiones Prov., Argentina, in MACN, examined. Brignoli, 1983:271.

Description.—*Female holotype:* Cephalothorax pale yellowish, cephalic region with some orange meandering marks. Chelicerae dusky proximally. Sternum light dusky. Femora with small black spots and distal black ring; patellae black ventrally. Abdomen white with anterior median black line below tip; posterior protuberances with black marks (Figs. 73, 74); venter without marks. Posterior median eyes 1.1 diameters of anterior medians, laterals 1 diameter. Anterior median eyes 1.3 diameters apart, 2.1 diameters from laterals. Posterior median eyes 1.1 diameters apart, 3 diameters from laterals. Ocular quadrangle square. Height of clypeus equals 0.7 diameter of anterior median eye. Abdomen drawn out to a single point, with two posterior bulges and tubercles (Figs. 73, 74). Total length 5.8. Carapace 3.1 mm long, 2.5 wide, 1.3 wide behind lateral eyes. First femur 3.2 mm, patella and tibia 4.1, metatarsus 2.0, tarsus 0.9. Second patella and tibia 3.1 mm, third 1.8, fourth 2.7. Abdomen 10 mm high.

Diagnosis.—*Kaira conica* differs from *K. candidissima* by having larger eyes, a longer abdomen (Figs. 73, 74) and a narrower sternum, which is as wide between the second and third coxa as between the first and second.

Specimens examined.—**BRAZIL**. *São Paulo:* Piracicaba, ♀ (MNRJ). *Rio Grande do Sul:* General Câmara, 19 Oct. 1982, imm. (E. H. Buckup, MCN 10902).

Kaira echinus Simon
Figs. 75–81; Map 2

Caira echinus Simon, 1895:478. Female holotype from Rio Salobro, Prov. Bahia [Bahia State], Brazil, in MNHN no. 8338, examined. Bonnet, 1956:925.
Kaira echinus: - Roewer, 1942:904.

Description.—*Female holotype:* Carapace orange-white with a dark reticulated patch on each side of cephalic region. Chelicerae, labium, endites orange-white. Sternum brownish black. Coxae, legs orange-white with black spots and patches. Dorsum of abdomen white with dusky and black spots and a pair of anterior black patches (Fig. 78); venter with black spots on white. Eyes subequal. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Height of clypeus equals 1.5 diameters of anterior median eye. Abdomen with humps and numerous paired tubercles of different lengths (Fig. 78). Total length 6.5 mm. Carapace 2.7 mm long, 2.5 wide, 1.2 behind lateral eyes. First femur 3.4 mm, patella and tibia 4.4, metatarsus 2.7, tarsus 1.1. Second patella and tibia 3.1 mm, third 2.0, fourth 2.5. Abdomen (estimate) 5.3 mm high.

Male from Paraná State, Brazil: Carapace brown, spotted with black and some yellowish patches. Sternum brown, black patches. Legs yellowish with brownish black rings. Dorsum of abdomen brown with black spots and patches (Fig. 81). Posterior median eyes 1.3 diameters of anterior medians, anterior laterals one diameter, posterior laterals one. Anterior median eyes 2.5 diameters apart, 2 diameters from laterals. Posterior median eyes 1.5 diameters apart, 1.5 diameters from laterals. Ocular quadrangle almost square, very slightly wider than long. Height of clypeus equal to 1 diameter of anterior median eye. Abdomen wider than long, with humps and paired tubercles (Fig. 81). Total length 2.5 mm. Carapace 1.40 mm long, 1.20 wide, 0.65 behind lateral eyes. First femur 1.62 mm, patella and tibia 1.89, metatarsus 1.14, tarsus 0.60. Second patella and tibia 1.56 mm, third 0.88, fourth 1.06. Abdomen 1.98 mm high.

Note: Males were matched with females because both have an abdomen that is wider than long.

Variation: Total length of males 2.3 to 2.6. Illustrations were made from the female holotype and a male from Paraná State.

Diagnosis.—The shape of the abdomen and its dark coloration separate the female from others. The eight teeth of the median apophysis and the row of denticles of the conductor of the palpus separate the male.

Specimens examined.—**BRAZIL**. *Paraná:* Guarapuava, Estância Santa Clara, 22 Nov. 1987, ♂ (A. D. Brescovit, MCN 17122). *Rio Grande do Sul:* Viamão, Morro do Côco, 9 Dec. 1982, ♂ (A. A. Lise, MCN 11308). **ARGENTINA**. *Misiones:* Eldorado, 1 Sept.–15 Nov. 1964, ♂ (A. Kovacs, AMNH).

Kaira hiteae Levi
Figs. 82–85; Map 2

Kaira hiteae Levi, 1977:220, figs. 138–140, ♂. Male holotype from Cove Creek Valley, 9.3 km W of Prairie Grove, Washington County, Arkansas, in MCZ. Brignoli, 1983:271.

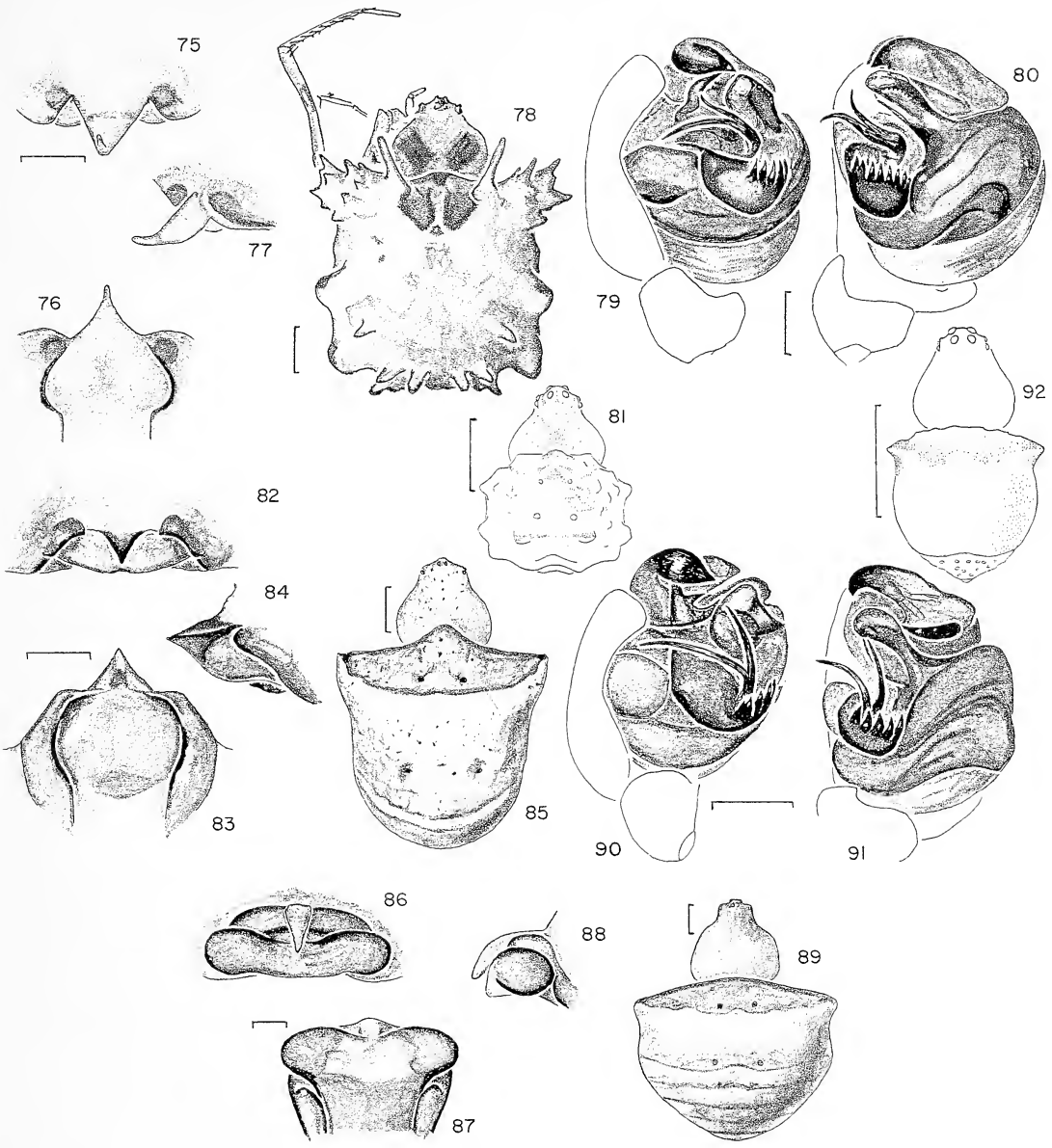
Description.—*Female from southern Texas:* Carapace pale yellow-white with scattered dark spots on cephalic region. Chelicerae pale yellowish with dusky spots. Labium, endites pale yellow. Sternum yellow. Coxae pale dusky yellow, legs yellow-white with brown rings and tiny brown spots. Anteriorly dorsum of abdomen dark between humps, posteriorly light, becoming darker, posteriorly except for a white transverse band (Fig. 85). Venter gray with tiny dark spots and white pigment spots. Eyes subequal. Anterior median eyes 1.3 diameters apart. Posterior median eyes their diameter apart. Posterior median eyes on slight swelling facing laterally and dorsally. Height of clypeus equals 1.5 diameters of anterior median eye. Chelicerae with three long teeth on anterior margin, three small teeth posterior. Abdomen shield-shaped (Fig. 85). Total length 6.2 mm. Carapace 2.8 mm long, 2.2 wide, 1.2 wide behind lateral eyes. First femur 3.4 mm, patella and tibia 4.3, metatarsus 2.5, tarsus 1.1. Second patella and tibia 3.1 mm, third 1.9, fourth 2.4. Abdomen 5.2 mm high.

Male: Description and illustration in Levi 1977: 220, figs. 138–140.

Note: Male and female have the abdomen similarly shaped.

Diagnosis.—The female is separated from other *Kaira* species by the shield-shaped abdomen (Fig. 85) and the triangular cross-section of the scape of the epigynum (Figs. 82–84).

Distribution.—Southeastern United States (Map 2).



Figures 75–92.—*Kaira* species: *K. echinus* (75–81); 75–78, female; 75–77, epigynum; 75, ventral; 76, posterior; 77, lateral; 78, dorsal; 79–81, male; 79, 80, left palpus; 79, mesal; 80, ventral; 81, dorsal. *K. hiteae*, female (82–85); 82–84, epigynum; 82, ventral; 83, posterior; 84, lateral; 85, dorsal. ***K. cobimcha*** (86–92); 86–89, female; 86–88, epigynum; 86, ventral; 87, posterior; 88, lateral; 89, dorsal; 90–92, male; 90, 91, palpus; 90, mesal; 91, ventral; 92, dorsal. Scale lines = 1.0 mm, of genitalia = 0.1 mm.

Natural History.—Padre Island, the collecting site of the female, is a xeric semibarren spit, windy and hot (W. Peck, pers. comm.).

Specimen examined.—**TEXAS**. *Cameron County:* South Padre Island, N Brazos Santiago Pass, sweeping vegetation, 10 Nov. 1979, ♀ (T. Allison, MCZ).

Kaira cobimcha new species
Figs. 86–92; Map 2

Holotype.—Male holotype from 260 km N of Xavantina, 12°49′S, 51°46′W, 400 m, Mato Grosso, Brazil (Xavantina-Cachimbo Expedi-

tion), in MCN ex MCZ. The specific name is an arbitrary combination of letters.

Description.—*Female:* Cephalothorax yellowish. Abdomen with a transverse dark area anterior of two humps, posteriorly with six dusky transverse lines (Fig. 89). Eyes subequal. Anterior median eyes 1 diameter apart, 2.5 diameters from laterals. Posterior median eyes 0.8 diameter apart, 3.2 diameters from laterals. Ocular quadrangle slightly narrower behind. Height of clypeus equals 1 diameter of anterior median eye. Abdomen shield-shaped, wider than long (Fig. 89). Total length 8.0 mm. Carapace 3.3 mm long, 3.1 wide, 1.3 behind lateral eyes. First femur 3.5, patella and tibia 4.9, metatarsus 2.5, tarsus 1.1. Second patella and tibia 3.7, third 2.1, fourth 2.9. Abdomen 5.5 mm high.

Male holotype: Carapace brown. Chelicerae, labium, endites brown. Sternum brown. Legs brown with white rings at proximal ends of third and fourth tarsi. Dorsum of abdomen mostly brown; anterior shield starting between humps, area posterior of shield black (Fig. 92). Venter black. Posterior median eyes 1.3 diameters of anterior medians, laterals 0.8 diameter. Anterior median eyes their diameter apart, 1.2 diameters from laterals. Posterior median eyes 0.8 diameter apart, 1.3 diameters from laterals. Ocular quadrangle square. Height of clypeus equals 0.7 diameter of anterior median eye. Abdomen shield-shaped, completely covered by a scutum anteriorly, with some tiny sclerotized spots posteriorly (Fig. 92). Scutum with punctate texture. Total length 1.8 mm. Carapace 0.92 mm long, 0.81 wide, 0.42 wide behind lateral eyes First femur 1.08 mm (distal articles and second legs lost). Third patella and tibia 0.62 mm, fourth 0.75. Abdomen 1.26 mm high.

Note: The female was matched to the male because of similarities in the shape of the abdomen (Figs. 89, 92). The abdomen of both were slightly lifted to make the illustrations.

Diagnosis.—The shape and markings of the abdomen (Fig. 89) resembles that of *K. sexta*. The epigynum differs by having two anterior tranverse bars in ventral view (Fig. 86), *K. sexta* shows only corners of the anterior bar (Levi 1991, fig. 339). The scape is hidden by setae. The male differs from others by the sclerotized plate on the abdomen (Fig. 92), and the shape of the conductor (center to 1100 h in Fig. 91).

Natural history.—The holotype was collected in campo-grassland.

Specimen examined.—**BRAZIL.** *Rio Grande do Sul:* Santa Maria, 10 Nov. 1990, ♀ (Linck, MCP).

Kaira sexta (Chamberlin), new combination
Map 2

Aranea sexta Chamberlin, 1916:255, pl. 19, fig. 7, imm. Immature female holotype from Panama, in MCZ, examined. Roewer, 1942:852.

Araneus sextus: Bonnet, 1955:598. Levi, 1991:259, figs. 339–342, ♀, ♂.

Note: The shape of the abdomen in females of *K. hiteae* and of *K. cobimcha* called to mind the strikingly similar *Araneus sextus*. On reexamination, *A. sextus* was found to have the legs modified as in species of *Kaira*, and is now transferred. The abdomen of *K. sexta* is the same shape as that of *K. cobimcha* (Fig. 89); the shape of the genitalia separate the species.

Kaira sabino Levi
Map 2

Kaira sabino Levi, 1977:221, figs. 141–147, map 3. Female holotype from Sabino [?Canyon, Pima County], Arizona in MCZ.

Distribution.—Southern Arizona.

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REVISION OF THE GENUS *TRECHALEA* THORELL (ARANEAE, TRECHALEIDAE) WITH A REVIEW OF THE TAXONOMY OF THE TRECHALEIDAE AND PISAURIDAE OF THE WESTERN HEMISPHERE

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ABSTRACT. The spider family Trechaleidae, introduced by Simon in 1898 but abandoned immediately thereafter, is defined. Characters proposed for trechaleids by recent authors for this family and some characters used to separate it from the Pisauridae and Lycosidae are reviewed. Genera included in the family Trechaleidae, all of which were previously placed in the Pisauridae, are: *Trechalea*, *Hesydrus*, *Syntrechalea*, *Dossenus*, *Paradossenus*, *Dyrines* and *Enna*. Familial placement of all other genera of the western hemisphere previously placed in the Pisauridae are considered.

The genus *Trechalea*, with eleven species, is revised. Redescriptions of eight known species are given: *T. longitarsis* (C. L. Koch), *T. cezariana* Mello-Leitão, *T. macconnelli* Pocock, *T. paucispina* di Caporiacco, *T. connexa* (O. Pickard-Cambridge), *T. extensa* (O. Pickard-Cambridge), *T. gertschi* Carico & Minch and *T. amazonica* F. Pickard-Cambridge. Descriptions of three new species: *T. boliviensis, T. lomalinda* and *T. trinidadensis* are presented. The holotype of the type species of *Trechalea*, *T. longitarsis*, is lost. The specimen which was previously regarded as the holotype is mislabelled and belongs actually to another, unnamed, trechaleid genus. All other relevant species names not synonymized with any of the above and not previously placed in *Trechalea* are removed to other known genera or will be later included in new genera.

In the early 1970's I began a series of revisions of the American Pisauridae with *Pisaurina* (Carico 1972) and *Dolomedes* (Carico 1973). The immediate goal was to clarify the taxonomy, at the genus and species levels, which would establish the required base for a later analysis at higher levels. The traditional family Pisauridae was retained as a matter of convenience with deferral until later of the re-examination of the family taxon itself.

While working on a group of primarily Neotropical genera, including *Trechalea*, I became aware that they represented a monophyletic clade which challenged the limits of the traditional family Pisauridae. This group of genera was therefore set aside for special consideration and was used as a basis for a study of the family-level taxonomy.

Of the seven genera placed here in the family Trechaleidae Simon, six were described around the turn of the century by Simon and the Pickard-Cambridges. These genera include *Hesydrus* Simon (1898a), *Syntrechalea* F. Pickard-Cambridge (1902), *Dossenus* Simon (1898b), *Paradossenus* F. Pickard-Cambridge (1903), *Dyrines* Simon (1903) and *Enna* O. Pickard-Cambridge (1897). *Trechalea* Thorell (1869) was described approximately thirty years earlier.

Simon apparently realized that he was studying a group of unique spiders when he, rather cryptically, inserted a two-line notation of the new family Trechaleidae in his summary of 1890. No description was offered and only the reference to two genera, *Dendrolycosa* and the type genus *Trechalea*, was given. He never again referred to this family and continued (1898) to name new species of the genus *Trechalea* in his old family Pisauridae.

During a meeting of the International Congress of Arachnology, I reintroduced the Trechaleidae (Carico 1986), erroneously referring to this family name as a *nomen oblitum*. At that time I presented a provisional cladogram showing its relationship to the families Pisauridae and Lycosidae, with the Pisauridae as the probable sister group.

The complexity of the Trechaleidae combined with the rather close relationship of the genera made it highly desirable that all possible material be examined before formal publication of a family analysis was attempted. Only after examining all available related type specimens and collec-

tions scattered in numerous museums was I able to sort out the genera and species. It then seemed necessary to revise the entire family at once before any generic revision could be published to provide what was believed to be the proper foundation for a secure set of family apomorphies. As a result, much time was required to bring the project to completion.

In the meantime, various authors have examined specimens of the family and have generally also concluded that the Trechaleidae represents a distinct group and is probably a valid family. Sierwald (1990), in her efforts to work out the higher taxonomy of the American Pisauridae, has shown through an excellent study of the male genitalia that the "*Trechalea* genus-group" represents a distinct taxon from the Pisauridae and that the Lycosidae is the probable sister group of her "*Trechalea* genus-group." Griswold (1993) confirmed, by a preliminary cladistic analysis of the Lycosoidea, the distinctness and monophyly of the Trechaleidae and placed the family as the sister group of the Lycosidae. Dondale (1986) listed family level synapomorphies for the Lycosidae, and further noted that the family shared some of these characters with *Trechalea*.

To date no complete treatment of the family has been presented nor have any of its included genera been revised. It is my intention in this paper to revise the genus *Trechalea* and to review the taxonomy of the family Trechaleidae in reference to the related families Pisauridae and Lycosidae. Later, revisions of the remaining six described genera and new genera will follow. A summary of their phylogenetic relationships and a key to their identification will also be presented at the appropriate time.

METHODS

Careful dissections of unexpanded palps were conducted to learn the relative positions of the various components, as in the approach of Dondale (1986). This method develops a good understanding of palpal structure that makes possible comparisons among different genera because all palpi in this unaltered condition are more likely to be similar. Expanded palpi were also studied, but expansion by its very nature, causes distortion in positional relationships which inevitably results because of difficulty in controlling the degree of expansion. Comparisons between specimens of different genera were therefore much more difficult on palpi in this state.

To study epigyna, the soft tissue was removed by a combination of dissection and immersion in KOH or a proteolytic enzyme. Since the internal parts were often dense and dark, they were immersed in Chlorox (sodium hypochlorite solution), as per the method of Griswold (1993), until only the internal lining of the ducts was uncleared. In addition, to trace better the tubules, the cleared, alcohol-saturated structure was allowed to air dry completely, which causes the silvery trace of the lumen to appear when the structure was reimmersed in alcohol.

Drawings were made with pen and ink, using a Bausch & Lomb Stereozoom® Microscope equipped with eyepiece drawing grid and micrometer. The right palp was illustrated from the ventral and retrolateral positions. SEM micrographs of the median apophysis and tibial retrolateral apophysis at ventral view are provided for comparison and diagnosis. Epigyna were drawn from the ventral view with setae removed, and from the dorsal view, uncleared, with the soft tissue removed.

Measurements are in mm. As an index to the size of the body, only the length of the carapace is given because of variability in the condition of the abdomen. Generally, the length of the abdomen is approximately equal to the carapace length in males while the abdomen may be somewhat longer in females. Eyes or eye group measurements were made with the surface plane perpendicular to the axis of sight. Abbreviations and additional notes pertaining to eye group measurements are in Table 1.

Museum abbreviations.—AMNH—American Museum of Natural History; BMNH—The Natural History Museum, London; CAS—California Academy of Sciences; EXPE—Exline-Peck (now in CAS); FMNH—Field Museum of Natural History; INPA—Instituto Naçional de Pesquisas Amazônia; JAK—J. A. Kochalka; JEC—J. E. Carico; MACN—Museo Argentino de Ciencias Naturales, Buenos Aires; MCN—Museu de Ciências Naturais, Fundação Zoobotânica do Río Grande do Sul; MECN—Museu Equitoriano de Ciencias Naturales, Ecuador; MEG—M. E. Galiano; MCZ—Museum of Comparative Zoology; MZUCR—Museo de Zoologia Universitaria, Costa Rica; REL—R. E. Leech; USNM—National Museum of Natural History.

Abbreviations of anatomical terms for genitalia.—Many anatomical terms and abbreviations of genitalia were adopted primarily from Sierwald (1989, 1990) while others were coined for

purposes of this paper: *ab*—accessory bulb of epigynum; *af*—anterior field of the epigynum; *bs*—base of spermatheca; *c*—conductor; *cd*—copulatory duct; *cdd*—copulatory duct diverticulum; *co*—copulatory opening; *cy*—cymbium; *dd*—dorsal division of median apophysis; *e*—embolus; *eb*—embolic base; *ecd*—ectal division of the retrolateral apophysis of the male palpal tibia; *epf*—epigynal fold; *eg*—embolic groove; *end*—ental division of the retrolateral apophysis of the male palpal tibia; *ep*—epigynal plate; *fd*—fertilization duct; *g*—guide (part of *ma*); *hs*—head of spermatheca; *ifa*—internal fold of anterior field; *ll*—lateral lobes; *ma*—median apophysis; *mf*—middle field of the epigynum; *p*—petiolus; *pma*—posterior margin of anterior field of epigynum; *rta*—retrolateral tibial apophysis; *s*—spermatheca; *sd*—sperm duct; *ss*—stalk of spermatheca; *st*—subtegulum; *t*—tegulum; *ti*—tibia; *vcm*—ventral cymbio-tibial membrane of the palpal tibia; *vd*—ventral division of median apophysis; *vp*—ventrodistal protuberance of male palpal tibia; *vr*—ventrodistal rim of male palpal tibia.

Family Trechaleidae Simon

Trechaleidae Simon, 1890:82, type genus *Trechalea* Thorell, 1869. Bonnet, 1955-1959:4680; Carico, 1986:305; Coddington & Levi, 1991:22, (cladogram); Griswold, 1993:1–39.
Dolomedeæ (in part), Simon, 1898a:301.
Dolomedidae (in part), Lehtinen, 1967:372.

Diagnosis.—The family Trechaleidae can be distinguished from the Lycosidae by the presence of: a retrolateral apophysis and a ventrodistal refolded rim on the male palpal tibia (Fig. 7), the posterior eye row (PE) in a single recurved row, and eyes in two rows.

In only the Pisauridae, in comparison with Lycosidae and Trechaleidae: the female produces a nursery web (a matrix of irregular webbing surrounding the egg sac and upon which the female sits and defends against intruders), in some species the male binds the female's front two pairs of legs with silk during copulation, and a unique tubular retreat with associated resting behavior is constructed by some species.

The Trechaleidae can be distinguished from both the Lycosidae and Pisauridae by: the male palpus which has a large distally situated median apophysis equipped with a dorsal embolic groove that extends distally into an apical guide (Fig. 7), the presence of a discoid egg sac carried only on the spinnerets, presence of a "skirt" on the seam of the discoid egg sac (Fig. 6), transport of young on the empty egg sac, and non-reattachment of dislodged egg sac.

Description.—Very large (body length up to 21 mm, leg span up to 167 mm; *Trechalea cezariana*) to small (body length down to 3.5 mm, leg span down to 18 mm; undescribed genus and species), entelegyne, araneomorph, ecribellate, lycosoid. Carapace low to moderately low, about as wide as long with cephalic area moderately distinct to indistinct, longitudinal fovea distinct. Eyes viewed from above in two rows, PE row recurved, subequal in size, approximately equidistant and separated by about an eye diameter, AE row straight or nearly so, always smaller than PE, ALE smaller than AME; ocular quadrangle wider above, about as high as wide. Clypeus height variable. Sternum about as wide as long, truncated anteriorly and acute posteriorly. Labium free, length-width ratio may be greater or lesser than 1.0. Chelicerae vertical, base robust, often enlarged anteriorly on males, promarginal teeth three, equidistant with middle one largest, retromarginal teeth variable between three and five in number varying in size and distribution. Endites longer than wide, parallel.

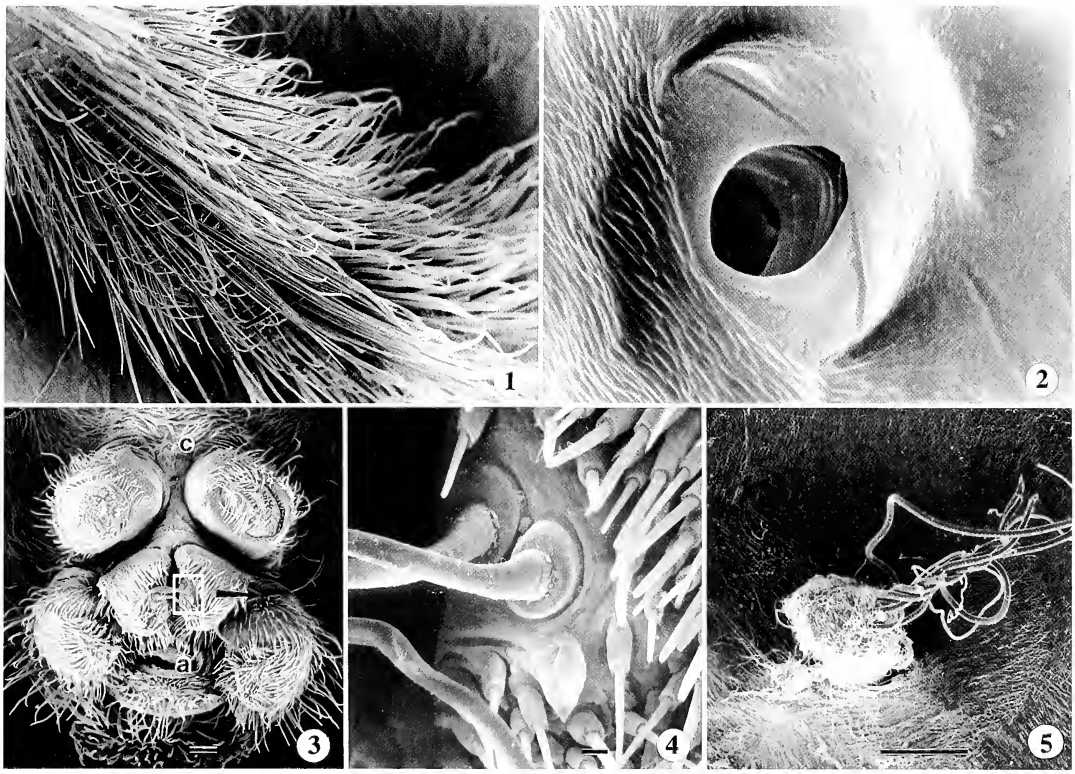
Abdomen oval, low, somewhat flattened ventrally, moderately covered with setae, often patch of setae present ventrally and anterior to spinnerets, no plumose setae found. Six spinnerets and colulus present. Tracheal spiracle located just anterior of colulus.

Male and female genitalia are described below.

Legs generally long, slender, often with flexible tarsi (Fig. 1), and, in some species, flexible metatarsi. Coxae notched ventrally. Third legs always shortest but relative lengths of other legs vary. Large macrosetae present on most segments, found in varying numbers of pairs on ventral surfaces of tibiae and metatarsi. Long setae, often curved at tips (Fig. 1), present mainly on ventral surface of legs. Trichobothria: tarsi with two rows and in alternating position, metatarsi with one row, tibia with cluster near proximal end with few others scattered distally, femur none. Bothrium (Fig. 2) with hood distinct, angled laterally, not ridged or embedded. Tarsi and metatarsi may be scopulate (Fig. 1) with one median and two lateral claws, all usually dentate. Female palpus with single, dentate claw.

Distribution.—The family is found entirely within the region from the Gila River of Arizona, United States southward to northern Argentina.

Natural history.—The included species have



Figures 1–5.—Scanning electron micrographs of structures of trechaleids: 1, 2, *Trechalea gertschi*; 1, tarsus, retrolateral view showing flexible integument and scopula; 2, bothrium; 3-5, *Hesydrus habilis*; 3, spinnerets (a = anal pore, c = colulus); 4, enlargement of 3 with emphasis on posterior median spinnerets, mesally located pairs of minor ampulate gland spigots with silk emerging from three of them; 5, attachment of four "carrying threads" to top valve of egg sac. Magnifications: 1, 60×; 2, 2000×. Scales: 3, 100μ; 4, 10μ; 5, 100μ.

a wide size range, and one would expect a wide divergence of habitat preferences to exist. Information is available, however, mainly for the larger species. The general impression from collection data and from personal observation is that the preferred habitat is around the margins of bodies of freshwater. Some moderate-sized species have been taken from trees and other vegetation away from water.

No species is known to make a snare of any kind and all are apparently entirely cursorial. The most aquatic species are very adept at walking on the water surface and crawling underwater in the manner familiar to the aquatic species of the pisaurid genus *Dolomedes* (Simon 1898a; pers. obs.). The feature of flexible tarsi is common in the family. The flexibility is due to a general softness of the cuticle rather than the occurrence of pseudosegmentation. This flexibility, which may be quite extensive, could be an advantage in the support and locomotion on the water surface.

No nursery web is constructed. The female carries the egg sac containing eggs or first instar spiderlings by the spinnerets, specifically the paired minor ampulate gland spigots on each posterior median spinneret (Figs. 3, 4, identified by J. Coddington, pers. comm.) in the manner of lycosids. The egg sac has a unique structure, described as hemispherical by Simon (1898a), with a generally flattened shape and with a distinct fringe or "skirt" at the seam between the two valves (Fig. 6). As the eggs hatch and the spiderlings occupy more of the internal space of the egg sac, the "skirt" is obliterated by stretching. The young emerge from the weak junction at this seam presumably without aid from the mother. After emergence, the young are carried upon the egg sac mostly on the upper valve but, with crowding above, also sometimes below. Young may also be found on the abdomen of the mother, but apparently only as a consequence of insufficient space on the egg sac and then only if they are in contact with sac-borne spiderlings. I

have not observed young only on the abdomen; when only a few young are present, they are only on the egg sac. The mother persists in carrying the egg sac and has been observed carrying it well after spiderlings have left. Only four strong lines are attached from the posterior median spinnerets to the center or near center of the upper valve, leaving a distinct single scar (Fig. 5). The female will not reattach the egg sac at any stage if it is dislodged. Both upper and lower valves are smooth on the surface, the upper usually darker and thicker while the lower is lighter, thinner, and flatter (Simon 1898a; Sierwald 1990; pers. obs.) with the eggs or young often visible.

Status of the type genus.—By reference to *Trechalea* as the type genus of the family Trechaleidae (Simon 1890), it follows that the family name therefore hinges on the type of its type species, *Trechalea longitarsis* (C. L. Koch). However, the correct identity of this species presents a problem.

C. L. Koch (1848) described a female from what is now known as Colombia with a body length of 7½ lines (= 15.7 mm, H. Levi pers. comm.) and gave it the name of *Triclaria longitarsis*. Some important distinctive features listed in his description included the pattern of the eyes (which were figured) and the "sickle-shaped" tarsi, both of which are important identifiers of what has traditionally been considered *Trechalea*. *Trechalea* was the name later given as a *nomen novum* by Thorell (1869) to the genus because the name *Triclaria* was preoccupied by a bird genus.

Later, Karsch (1879) found a dried spider in the Berlin Museum, no. 2006, which he regarded as the specimen Koch used when making the description of *Triclaria longitarsis* because of Koch's reference to the "sickle-shaped" tarsi. Karsch mentioned two labels with the specimen, one of which states "Brasilien, Langsdorff" and the other simply as "longitarsis?". Noting the discrepancy of the published locality as "Colombia" and the label contained with the specimen as "Brazil," he dismissed it merely as a change made presumably in curating. Kraus (1955) agreed with Karsch's conclusion.

I have examined the specimen no. 2006 mentioned by Karsch and found the following: (a) The specimen is a juvenile with the body length of 12.2 mm, presently preserved in alcohol, but was apparently originally mounted dry. The presence of a hole through the carapace and sternum indicates that it was probably perforated with a pin. Only a single entire leg is still attached; others are shattered. (b) The vial contains a total of five labels which are as follows: "2006", "longitarsis Koch?", "Brazilien Lgsof", "Typus", and a modern label which has the number, species name, etc., and the notation, "(*sensu* Karsch)". The first three of these labels have pin perforations (two of which were mentioned by Karsch) and were presumably pinned originally with the specimen. The "Typus" and modern label, which were not perforated, were apparently added with the specimen after it was placed into alcohol storage.

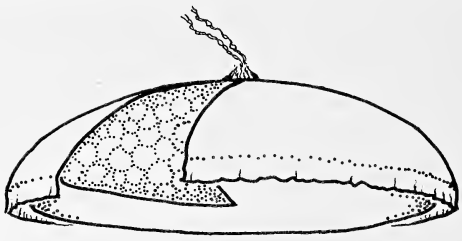


Figure 6.—Diagram of a trechaleid egg sac with "carrying threads" attached.

After careful consideration of the evidence, I have concluded that this specimen, hereafter referred to as "2006," is not the type specimen for *Trechalea longitarsis* (Koch). My conclusion is based on the following observations: (1) Koch indicated that his specimen was a "female", presumably meaning it was adult. "2006" is a juvenile. (However, these authors, including Simon, often assumed that juveniles were females and did not look for an epigynum [Levi, pers. comm.].) (2) Koch stated that the length of his specimen is "7½‴", (or 15.7 mm). "2006" is 12.2 mm, which is significantly shorter. (3) An examination of the external characters of "2006" shows it to be a member of a new genus (which will be described in a later publication) with a distinctive carapace shape, and offset fifth retromarginal cheliceral tooth. As will be shown later, this genus is found only in the southernmost states of Brazil in the Río de la Plata drainage system, far from Colombia. Therefore, "2006" is not from Colombia, and the specimen label which has the locality "Brasilien" is probably correct. (4) The label in the vial with "2006", "longitarsis Koch?," placed after Koch's description and before Karsch's discovery, indicates that the person who pinned the label to the specimen had doubts about it, as indicated by the question mark. Therefore, uncertainty about the specimen apparently pre-

dates Karsch. (5) The "Typus" label was added after Koch, because it lacks the perforation and does not add proof that Koch made this designation himself about this particular specimen. The conclusion that this specimen was the type could have been based on the assumptions of Karsch and may have actually been added, incorrectly, by him. (6) Karsch's conclusion was apparently promoted by the lack of other material available to him for comparison combined with an overemphasis on the distinct eye and tarsus characters that led him to make the statement that "2006" agrees exactly with the description.

The partially insect-eaten, dried, and presumably faded specimen after 30 years must have lost much of the detail, especially pattern, of the fresh specimen. Thus, the conclusion of Karsch may have been influenced by the combination of a process of elimination, misleading labels, and an overemphasis on the few distinct characters remaining on the specimen.

The above evidence leads me to conclude that "2006" is not the holotype specimen of *Triclaria longitarsis* designated by Koch. With this conclusion, one is still left with the problem about the status of the nomenclature of the genus and thus of the family. In order to provide stability of the names, I make certain assumptions based on the examination of a considerable amount of material.

I assume that the type specimen is lost and that Colombia was the actual type locality as stated by Koch. Furthermore, I assume that the most probable part of the country where the specimen was taken is that area of northern Colombia extending from the Atlantic coast to Bogotá, the most likely area that a European collector might visit. Thus, the presumed type locality is in the coastal drainage region rather than in the Amazonian drainage area. As explained later, these two drainages have distinct species of *Trechalea* which fall into the size range stated by Koch. Therefore, the *Trechalea* species found in the coastal area, is assumed to be *T. longitarsis*.

Status of unrevised "pisaurid" genera in the Western Hemisphere.—Since this work brings about some reassignments of a major group of genera from the Pisauridae (or Dolomedidae) to the Trechaleidae, it is appropriate now to summarize the familial placement of the remaining unrevised "pisaurid" genera in the Western Hemisphere. The remainder of this section is devoted to my determination of the disposition of these genera based on an examination of the available types.

Tunabo Chamberlin (1916) is based on an immature male holotype and is a lycosid (confirmed by H. Levi pers. comm.) but was regarded as a zorid by Lehtinen (1967) and was therefore listed in the latter family by Brignoli (1983) and Platnick (1989). *Sisenna* Simon (1898a) is a junior synonym of *Architis* and is treated elsewhere (Carico 1993). Two species described by Keyserling in the genus *Tetragonopthalma* Karsch (1878), *T. granadensis* (1877) and *T. obscura* (1891), are in the lycosid genus *Porrimosa* (Capocasale 1982). *Aglaoctenus* Tullgren 1905 is a junior synonym of *Porrimosa* (NEW SYNONYMY), a decision based on an examination of the holotype of *Aglaoctenus bifasciatus* Tullgren. The genus *Dyrinoides* Badcock (1932) was described for two species which are represented by tiny, unidentifiable spiderlings; however, they may be trechaleids. *Thaumasia* Perty (1833) is a pisaurid.

The Mello-Leitão genera *Xingusiella* (1940a) and *Demolodos* (1943) (*Demelodos* [*sic*] Mello-Leitão 1943; *Demolodes* [*sic*] Roewer 1954; Brignoli 1983; Platnick 1989) are each represented by a single species, and their types are lost in the Río de Janeiro museum and are not available for examination.

A species ascribed to *Nilus* (O. Pickard-Cambridge 1876), *N. amazonicus*, was described by Simon (1898b) from the Amazon region of Brazil. The type is a large, recently molted juvenile of unknown sex which is unlike any known American pisaurid and is not a trechaleid. Since the genus is otherwise known only from Africa eastward through Australia and Simon described many spiders from other continents in his 1898b publication, it is likely that this specimen was from another area and its locality is in error.

Two species of a primarily African and Asian genus, *Hygropoda* Thorell (1895), were described by Simon (1898a) from South America. Examination of the types of these species, *H. andina* and *H. venezuelana*, shows that they actually belong to the genus *Paradossenus*.

Ancylometes Bertkau (1880) bears some ctenid anatomical characteristics, but it is probably a pisaurid because of its clearly pisaurid behavior (Merrett 1988). A study of its relationships should be conducted, but is beyond the scope of this paper.

Status of various pisaurid species assigned to revised genera of the Western Hemisphere.—

During this study, no specimen of the widely distributed genus *Dolomedes* has been found from anywhere south of the Yucatan Peninsula. This confirms the opinion of Carico (1973) that the genus has only a Nearctic distribution in the Western Hemisphere with the exception of areas of southern Mexico. There are, however, a few species in the older literature described from South America which I have considered. Giebel's (1863) description of the eyes of his *Dolomedes intermedius* from Colombia clearly suggests that it is not a *Dolomedes*. I cannot determine its genus, however, because the holotype has not been found. The holotype of *Dolomedes albicoxa* Bertkau (1880) is lost but a reading of the description indicates that this species is not a *Dolomedes* because of the strongly procurved anterior eye row and relative sizes of the eyes. It may be a *Porrimosa* or a species of *Architis*. Although the holotype of *Dolomedes pullatus* Nicolet (1849) is missing, the description of the color pattern suggests to me that this species may be a *Thaumasia*. The holotype of *Dolomedes elegens* Taczanowski (1873) is missing, but the description of the color pattern gives very good indication that it is a *Thaumasia*.

Thanatidius spinipes F. O. Pickard-Cambridge (1903:156, 157) is a junior synonym of *Staberius spinipes* (Taczanowski). NEW SYNONYMY. All of the species of *Thanatidius* listed by Bonnet (1955–1959) have been synonymized. The genus was synonymized earlier by Carico (1972) to the entirely Nearctic genus *Pisaurina*.

Previous attempts at higher taxonomy.—Removal of these seven genera from the Pisauridae (*sensu* Simon) (*Trechalea*, *Hesydrus*, *Syntrechalea*, *Dossenus*, *Paradossenus*, *Dyrines*, *Enna*) into a monophyletic family is accompanied below by an historical examination of previous schemes of higher taxonomy. At least three authors have made a significant attempt to name families or subfamilies in which these genera were included.

Simon's (1898a) placement of *Trechalea*, *Hesydrus*, *Dossenus*, *Drances* (= *Dyrines*), and *Hygropoda* into "Dolomedeæ" (along with other genera), indicates his concept that these trechaleid genera are closely related. However, only the American species of *Hygropoda* are trechaleids as indicated above.

Roewer (1954) assigned the genera *Dossenus*, *Dyrines*, *Hesydrus*, *Paradossenus*, *Syntrechalea* and *Trechalea* to his Thaumasiinae. However, he assigned *Enna* to his Pisaurinae.

Lehtinen's (1967) attempt to place these genera into subfamilies and into new families resulted in the following: *Trechalea* ("..Lycosoidea *incertae sedis*; probably related to Zoridae, especially *Neoctenus*."), *Dossenus* (Dolomedidae), *Dyrines* (Dolomedidae), *Hesydrus* (Dolomedidae), *Paradossenus* (Dolomedidae), *Syntrechalea* ("Position obscure, but evidently a representative of Lycosoidea."). Additionally, genera which were previously assigned to Pisauridae are assigned as follows: *Xingusiella* (Amaurobiidae: Rhoicininae), *Aglaoctenus* (Dolomedidae) and *Dyrinoides* (Lycosoidea incertae sedis).

STRUCTURE OF THE GENITALIA IN *TRECHALEA*

Male palpus.—The basic structure of the male palpus of *Trechalea* was described by Sierwald (1990) in her survey of various pisaurid genera. Many of her conclusions and abbreviations concerning structure are used here; a more detailed description of the anatomy is available in her paper. Additional details were pointed out by Dondale (pers. comm.).

Basically, there are four, major, articulating, sclerotized elements which make up the bulb of the male palpus, each separated by membrane(s) (Fig. 7). Beginning at the base is the 1) *subtegulum* (*st*), attached to the *cymbium* (*c*) by a large membrane, the basal hematodocha (bearing within its wall the sclerotized petiolus). Next, moving distally, one encounters the ring-like 2) *tegulum* (*t*), described by Sierwald (1990) as having several loops or "switchbacks" of the sperm duct. Attached to the membrane distal to the tegulum is the large, conspicuous, 3) *median apophysis* (*ma*), and the 4) *embolus* (*e*) which is a thin, curved structure with a broad, subdivided base (*embolic base*, *eb*; [perhaps incorporating the terminal apophysis]). The embolic base is partly subdivided by a narrow membrane. Of these, only the embolus is not usually visible when viewed ventrally in the unexpanded state.

The median apophysis is a large, complex structure that appears to have a unique form in the trechaleids (Sierwald 1990) and is located distally on the bulb where it characteristically occupies about a fourth to a third of the bulb mass. On its dorsal side is a deep, narrow, longitudinal groove, the *embolic groove* (*eg*), in which the thin part of the embolus rests and is apparently comparable to that found in some lycosids (Dondale & Redner 1983b; Roth 1985 [key]). This groove (independently discovered by Don-

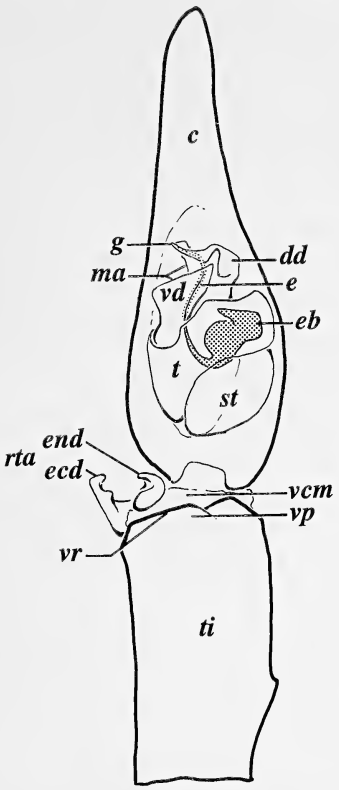


Figure 7.—Trechaleid palpus anatomy based on *Trechalea longitarsis*, ventral view. Embolus with its large embolic base in shading behind (dorsad) and showing the narrow part contained in the embolic groove of the median apophysis. Abbreviations in methods section.

dale, pers. comm.) continues distally into a curved or hooked projection arising from the *dorsal division* (*dd*), which probably serves as a *guide* (*g*) for the embolus during intromission (as is the case in some lycosids [Dondale & Redner 1978]) but seems not to support or protect the embolus at rest as with, respectively, the fulcrum and conductor found in, e. g., *Dolomedes*. In addition to the dorsal division, there is the conspicuous subdivision on the ventral side (*ventral division*, (*vd*) which varies in size and shape. The shape and position of the projections arising from these divisions are highly genus- and species-specific and are given special attention in the description and figures for each genus and species.

The *palpal tibia* (*ti*) bears a distal *retrolateral apophysis* (*rta*), which in some genera may be subdivided into two parts: the *ental division* (*end*) which is surrounded by membrane (defined below), and the *ectal division* (*ecd*) usually located laterally and proximally to the ental division. The size and shape of the retrolateral apophysis is genus- and species-specific. In addition to the retrolateral apophysis, there is a feature of the ventrodistal margin of the tibia in which the border folds down upon itself forming a depression down into the distal end of the tibia. This pit thus formed has been used as a taxonomic character of some importance by some workers (Sierwald 1990; Griswold 1993). See the section below on character analysis for further discussion of this feature and additional features of the tibia, *ventrodistal rim* (*vr*), and *ventrodistal protuberance* (*vp*), and *ventral cymbio-tibial membrane* (*vcm*).

Sierwald (1990) identified in the palpal bulbs of species of *Trechalea* and *Paradossenus* additional structures such as a conductor, terminal apophysis, etc., which are not used here for diagnostic purposes. Refer to her paper for a discussion of these details.

Female epigynum.—A thorough study of the homologies of the structures of the female genitalia is beyond the scope of the present analysis and the terminology used here is adapted from the work of Sierwald (1989) on American pisaurid genera. Emphasis is here directed to identification of major components and unique features of the genitalia of only *Trechalea* for diagnostic purposes. A preliminary survey of various trechaleid genera reveals a considerable range of variation, and each one will be treated individually later. Thus, broad generalizations concerning the family or any assortment of genera within it are left to work in progress. For descriptive purposes, terms are coined for use in *Trechalea* and may or may not be applicable to other members of the family.

The epigynum is generally heavily sclerotized (*T. trinidadensis* excepted), dark and opaque, with some components fused together, which makes detailed observation difficult without initial clearing. The external *epigynal plate* (*ep*) (Fig. 8) is composed of four regional elements, two *lateral lobes* (*ll*) which comprise the elevated portions on either side, an *anterior field* (*af*) which occupies most of the anterior half of the epigynum and is usually continuous with, but not always distinct from, the lateral lobes. The *middle field* (*mf*) is a distinct, posterior, median component set off from the other components by furrows and/or the *posterior margin of anterior field* (*pma*). (The "external, outer lateral margin of the epigynal fold" described by Sierwald (1989) for pisaurids appears in trechaleids to be round-

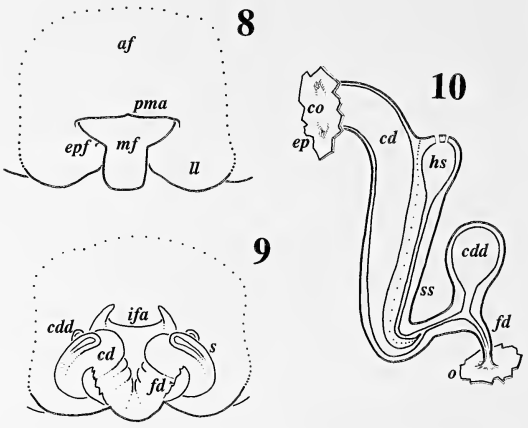
ed, less distinct and to lie out of sight under [dorsad to] the *mf*.) The relative shapes and dimensions of these components tend to be species-specific and are illustrated.

Internally (Figs. 9, 10), on each side, a generally large, voluminous *copulatory duct* (*cd*) arises from the anterior portion of the *epigynal fold* (*epf*) at the *copulatory opening* (*co*) and curves inward and posteriorly where it gives rise to a *spermathecum* (*s*) composed of a terminal enlargement (*head of spermatheca*, *hs*) at the end of a stalk (*stalk of spermatheca*, *ss*), most of which lies fused against the copulatory duct. A second diverticulum, called the *copulatory duct diverticulum* (*cdd*) arises secondarily from the copulatory duct. Although the function of this structure is unknown, its presence has been noted by Griswold (1993; "lobate spermathecal base", character #39). My interpretation of its relative position (between *ss* and *fd*), however, departs from his. I have been unable to find this structure in all trechaleids, except, e. g., a species of *Dossenus*. A *fertilization duct* (*fd*) continues from this junction to meet the *oviduct* (*o*) on its ventral side. An *internal fold of the anterior field* (*ifa*) in the shape of a thin flap (called "wing" by Sierwald) occurs in various shapes and is most conspicuous laterally where it joins the *cd*.

CRITICAL REVIEW OF SOME TAXONOMIC CHARACTERS USED IN RELATED FAMILIES

Since I reintroduced the family Trechaleidae (Carico 1986), it has been the independent opinion of Sierwald (1989, 1990), and Griswold (1993), that the Trechaleidae (or the "*Trechalea* genus-group") deserves family status and has as its nearest relatives the families Pisauridae and Lycosidae, with Lycosidae the closer. Coddington & Levi (1991) adopted the conclusions of Griswold and used the family name Trechaleidae. Additionally, Dondale (1986) emphasized in *Trechalea* its unique and lycosid-like features in his description of the subfamilies of the Lycosidae.

The Pisauridae, as currently constituted, appears to be a very complex group and may not be monophyletic. Sierwald, in her excellent studies of the American pisaurid female copulatory organs (1989) and male palpal organs (1990), stated that the known genera are apparently polyphyletic, a conclusion with which I agree. In contrast, however, monophyly was assumed for Lycosidae by Dondale (1986), who proposed a group



Figures 8–10.—*Trechalea* epigynum anatomy based on *T. longitarsis*: 8, epigynal plate, ventral view; 9, internal structures, dorsal view; 10, diagram of relative positions of internal structures. Abbreviations in methods section.

of synapomorphies for that family and proceeded further to define a number of subfamilies.

Griswold (1993) presented a wide-ranging but preliminary analysis of the Lycosoidea and included as exemplars in his cladogram members of the Pisauridae (*Dolomedes tenebrosus* Hentz, *Pisaura mirabilis* (Clerck)), Lycosidae (*Lycosa helluo* Walck., *Sosippus placidus* Brady), and the Trechaleidae (*Trechalea* sp.). The controversial genus *Rhoicinus* (Rhoicininae), considered a possible trechaleid by Sierwald (1990), was included. In his cladogram, a total of 20 apomorphies emerged to distinguish the six exemplars of these three families.

Both Sierwald (1990) and Griswold (1993) considered rhoicinines to be related to the trechaleids. The latter author included an undescribed *Rhoicinus* in his cladogram which emerged as a sister group to his genus *Trechalea* sp. and therein implied the two could be considered members of the Trechaleidae. Because of the problems historically in assigning a family for rhoicinines (Platnick 1979), the perceived weakness of Griswold's synapomorphies (discussed below), and the diversity of characters among the various genera currently assigned to the group (Exline 1960), I do not include rhoicinines in the Trechaleidae. However, I do not exclude the possibility of the family being broadened later to include rhoicinines as well as other genera, e. g., *Shinobius* of Yaginuma (1991).

In any case, the conclusions here must be considered provisional pending the outcome of on-

going studies by various workers who are continuing to revise the genera within these families. Such work is required to reveal consistent characters which contribute to greater confidence in whatever conclusion is reached about systematic relationships. Therefore, no cladistic analysis is offered here.

Following is a discussion of the taxonomic characters used to distinguish the families Trechaleidae relative to Pisauridae and Lycosidae used by recent workers (Dondale 1986; Sierwald 1989, 1990; Griswold 1993) including some offered here for the first time.

PLE situated behind PME to form a third row of eyes.—This character is a traditional one used to separate lycosids from the pisaurids. It is mentioned by Dondale (1986) and Sierwald (1990), and Griswold (1993).

Retrolateral apophysis on the male palpal tibia.—This is also a long-standing character used to separate pisaurids and lycosids and is mentioned by Dondale (1986), Sierwald (1990) and Griswold (1993). Separately, Dondale (1986) assumed that the loss of a retrolateral apophysis in the lycosids is a derived state. It is present in Trechaleidae and Pisauridae.

Median apophysis position on bulb.—This character is offered here for the first time and refers to the position of the median apophysis on the palpal bulb as viewed from the ventral side. The position is either somewhere on the ventral face, e. g., Lycosidae and Pisauridae, or, in the case of trechaleids, enlarged and occupying the distal fourth or third portion of the bulb mass.

Folded ventrodistal rim of the male tibia.—This is a reinterpretation of a so-called "pit" located ventrally at the apical end of male palpal tibia reported by others. Attention to a pit perhaps began with a feature noted in *Rhoicinus* by Exline (1960) who described it as an "unsclerotized pit, surrounded by a fairly high, rebordered, chitinous ring." A "membranous pit that accompanies the tibial apophysis" was noted later by Sierwald (1990) also in *Trechalea*, and she proposed that this may be synapomorphous for the two genera. Recently Yaginuma (1991, pp. 2, 4) noted a similar feature in a Japanese spider *Shinobius orientalis* (Yaginuma) and thus assigned this spider to the Rhoicininae in the Pisauridae with reservation. Griswold (1993) used a similar character in his analysis of lycosoids and named it as, "Male palpal tibia with retroapical cuticle unsclerotized." He used this as an important character to link both *Rhoicinus* and *Trechalea* together in his cladogram with the implication that the former genus was a trechaleid.

An examination of *Rhoicinus*, however, reveals that there is indeed a "ring" present, but the cuticle enclosed is actually sclerotized and the whole structure is situated on the sclerotized portion of the tibia. This ring and its enclosed cuticle are not synonymous with the "membranous pit" in the trechaleids as reported by these latter workers and is actually homologous with the retrolateral apophysis (*rta*) of trechaleids and pisaurids.

In the Trechaleidae (as here defined), another type of pit (not found in *Rhoicinus*) is actually formed from the *ventral cymbio-tibial membrane* (*vcm*, Fig. 7) of the male palpal tibia. This membrane, found in all spiders, may be broad and flexible to permit a wide arc of flexion at the articulation between the cymbium and tibia. It is not uncommon to note a concavity of varying degrees in this soft membrane in spiders of all three families. Since this concavity results from varying conditions of preservation, it is thus not taxonomically significant. The pit of *Trechalea* referred to by the previously-mentioned authors, however, is due less to a condition of the membrane itself, but rather to the morphology of the adjoining sclerotized *ventrodistal rim* (*vr*) (Fig. 7) of the tibia. In the trechaleids and, to a lesser degree, the pisaurids, there is a folding back downward of the rim into the inside of the cylindrical tibia, forming a noticeable depression in the ventral and retroventral end of the tibia because the *vcm* typically arises from this deep recess. In these same two families, the rim is usually also molded into a *ventrodistal protuberance* (*vp*) and thus forms a characteristic shape to the tibial rim from ventral view. No such rim or protuberance is found in American lycosids. What makes the so-called pit more noticeable in the trechaleids is that the distal, gaping opening of the cylindrical tibia is larger, and the dorsoventral elongation is accentuated by the *vp*.

Method of egg sac transport.—I depart from other workers in the interpretation and use of this character. The traditional approach has been to state the choice between "carrying egg sac in chelicerae" or "carrying egg sac on spinnerets". This is similar to Griswold's (1993) character #68 and is mentioned by Sierwald (1990) and Dondale (1986). This seems an oversimplification and inaccuracy because in all three families the females carry the egg sac attached to the spinnerets. Therefore, the pisaurids, which alone em-

ploy the chelicerae in transport of the egg sac, also carry it simultaneously with the spinnerets; this important fact is often overlooked. There are examples of carrying the egg sac in the chelicerae only in such diverse families as Pholcidae (Kaston 1948, p. 67) and Synotaxidae (*Mangua gunni* Forster et al. 1990, p. 76) and thus is not equivalent to the case with pisaurids.

Egg sac transport by spinnerets alone is commonly associated with lycosids but is also reported in trechaleids (Simon 1898a, *Trechalea*, *Hesydrus*, etc.; Van Berkum 1982, *Trechalea extensa*; Carico et al. 1985, *Trechalea amazonica*; Carico pers. obs., *Trechalea extensa*, *T. gertschi*, *Hesydrus habilis*).

Therefore use of the spinnerets to carry the egg sac is apparently plesiomorphic for all three families. The apomorphy customarily stated as "egg sac transported in chelicerae" in the context of the current discussion is more accurately restated by combining the two attachments, as is the case in the pisaurids.

Structure of egg sac seam.—It is assumed that during the construction of the egg sac in all three families, a seam is made because of the typical sequence of egg laying, i. e., lower sheet construction, followed by egg mass deposition and upper sheet construction. Specifically considered here, however, is the seam appearance when the egg sac is full of eggs (not hatchlings) after construction is complete. The appearances differ in all three families: seam apparent on spherical egg sac without "skirt" (lycosids), seam apparent as a rim on discoid egg sac with a "skirt" (trechaleids) (Fig. 6), seam not apparent on spherical egg sac (pisaurids).

Method of maternal care of young after emergence from egg sac.—Some form of maternal care is characteristic of all three families, but each family has a distinct method of caring for young. Trechaleids transport young on an empty egg sac. The young congregate on the empty egg sac which the female continues to carry until after the young disperse. However, as has been noted by Carico et al. (1985), transport of young on the abdomen has been observed in the trechaleids. Caution must be used in applying this character to the trechaleids because, in my observations, the presence of some spiderlings on the mother's abdomen seems only to occur when they are crowded and pushed off the egg sac. Therefore, young on the abdomen of trechaleids appears incidental and not synonymous with young transport on the abdomen in lycosids. Transport of young on the mother's abdomen is a character which is typically associated with lycosids, and in Dondale's (1986) list it is associated with transport of the egg sac on the spinnerets. It is important to note that Yaginuma (1991) reported that three Japanese lycosids, as well as his rhoicinine, *Shinobius*, carry the young on the egg sac. The nursery web is one of the most traditional characters of the family Pisauridae and has promoted the term "nursery-web spiders" for this group. This is mentioned by Carico (1973) and Sierwald (1990). It is Griswold's (1993) character #67.

Binding of female's front two pairs of legs by male during copulation.—Use of a bridal veil of silk by the male during copulation is widespread though apparently uncommon in spiders (Schmitt 1992). In the families here under consideration, only the pisaurids *Pisaurina mira* (Bruce & Carico 1988), *Ancylometes bogotensis* (Merrett 1988), and *Dolomedes triton* (Wojcicki 1990) are reported to use this behavior. In these three genera a unique type of veil is used, which has the structure spun only over the first two pairs of legs.

Web retreat.—Trechaleids are not known to build webs or retreats of any kind. Some lycosids are known to build webs with tubular retreats (Brady 1962). A distinctive structure of the pisaurid retreat, when present, is the characteristic short tube with the openings distinctively flared that has been found in another disparate group of pisaurid genera: *Pisaura mirabilis* (Lenler-Erikson 1969), *Pisaurina mira* (Carico 1985), and *Architis nitidopilosa* (Nentwig 1985). This retreat may be found only as a juvenile web in *P. mirabilis* and *P. mira* or as a more extensive web in the adult *A. nitidopilosa*. The spider rests with its body at right angles to the axis of the tube with its legs resting in the flared openings.

Reattachment of egg sac.—Female lycosids and pisaurids are well-known to reattach the egg sac if it is dislodged. In the trechaleids I have observed, *Trechalea gertschi*, *T. extensa*, and *Hesydrus habilis*, the egg sacs were never reattached to the spinnerets. On examination of upper surfaces of several egg sacs of these and other species, only a single, conspicuous attachment disc is ever present, although a zig-zag pattern of these "carrying threads" across the surface may be produced before final attachment.

Additional characters.—In Griswold's (1993) extensive character set, 14 additional new morphological synapomorphies were utilized in his cladistic analysis to distinguish these three families from each other and from the other families

of the Lycosoidea. Because their use has been applied only to the six exemplars and their universalities have not been tested in other genera of these families, they are not discussed further in the present study.

Sierwald (1990) referred to the "small, reduced conductor" (p. 51) as a synapomorphy for the "*Trechalea* genus-group". Because this structure in pisaurids ranges in size from the "large and strongly sclerotized. . .conductor in *Tinus*. . ." to "a low hump or prominence, as the conductor in *Architis*. . ." (p. 18) it is a difficult character to use. Her observation of "a median apophysis with two branches. . ." in this genus-group (p. 50) is difficult to apply because the median apophyses of some trechaleids have more than two while many lycosids have two branches, although they may not be of the same form as in trechaleids. She also observed that the "sperm duct with several switchbacks. . ." (p. 50) is a synapomorphy. If a switchback is defined as loop wherein the tube reverses its direction, then it is present in *Trechalea* and some other larger trechaleids, but smaller trechaleids such as *Dyrines* (p. 35) have only one or none in an undescribed genus. There are a number of undulations of the sperm duct which are also found in *Staberius*, a pisaurid (1990, fig. 25) and some local lycosids.

Genus *Trechalea* Thorell

Triclaria C. L. Koch, 1848:101, (type species by original designation, *Triclaria longitarsis* C. L. Koch).

Trechalea Thorell, 1869:37, (*nomen novum* for *Triclaria*, preoccupied). Simon, 1898a:279–281, 304–312, 315. Roewer, 1954, 2a:142. Bonnet, 1955–1959, II:4678. Lehtinen, 1967:379 (genus *incertae sedis*). Brignoli, 1983:461. Platnick, 1989:398.

Perissoblemma O. Pick.-Cambridge, 1881:773. First synonymized by Simon 1898a:311.

Diagnosis.—*Trechalea* can be distinguished from *Syntrechalea* by the fewer number of ventral tibial macrosetae pairs (4–6) while the latter has about twice as many. Also, *Trechalea* can be distinguished from *Hesydrus*, its closest relative, by having only the tarsi flexible while the latter genus has also the metatarsi flexible. The middle field of the epigynum in *Trechalea* is relatively short and lobe-like while that of *Hesydrus* tends to be longer and scape-like.

Description.—Carapace moderately low, cephalic area relatively distinct, AE row straight or slightly recurved when seen from above. Retromarginal cheliceral teeth ranging from 3–5, variable in size and distance. Leg relative lengths variable but III always shortest and IV almost always longest, only tarsi flexible, scopula may be present on metatarsus and tarsus, all claws dentate, pairs of macrosetae on ventral side of tibia I ranging from 4–6.

Male palpal bulb median apophysis with acute, conspicuous guide, ventral division variable but thickened, tibial retrolateral apophysis divided with ental division distinct, often lobed and partly surrounded by ventral cymbio-tibial membrane, ectal division conspicuous and in various forms.

Female epigynal plate with middle field about as wide as long or only slightly longer than wide, usually widest anteriorly (Fig. 8).

Distribution.—Found from the Gila River drainage system of central Arizona, United States southward to the state of Río Grande do Sul, Brazil.

Natural history.—Most members of this genus are found on the margins of freshwater streams and lakes. Many species are restricted to a particular river drainage system.

Disposition of nominal species of *Trechalea*.—*Trechalea ornata* Mello-Leitão (1943), *Trechalea wygodzinski* Soares and Carmargo (1948), *Trechalea keyserlingi* F. Pickard-Cambridge (1903), and *Trechalea biocellata* Mello-Leitão (1926) are being transferred to new trechaleid genera.

Trechalea reimoseri Caporiacco (1947) is represented by two syntypes, neither of which is a *Trechalea*, each belonging to different genus. The female is a *Syntrechalea* and the male is in an undescribed trechaleid genus. *Trechalea protenta* Karsch (1879) is transferred to *Paradossenus*. *Trechalea thomisiformis* (O. Pickard-Cambridge, 1881) is a very small juvenile lycosoid and appears not to be a trechaleid, but of doubtful genus. *Trechalea monticola* Chamberlin (1916) is transferred to *Hesydrus*.

Unsuccessful efforts were made to obtain certain holotypes of various species described by Mello-Leitão. The provisional determination of their status is made as follows: both *Trechalea syntrechaloides* Mello-Leitão (1940b, type #41476) and *T. limai* Mello-Leitão (1940b) appear from drawings and descriptions to belong to a new unnamed trechaleid genus. *T. aurantia* Mello-Leitão (1942) may be a *Hesydrus*. The generic status of *T. numida* Mello-Leitão (1943) and *T. langei* Mello-Leitão (1947) cannot be determined from their descriptions.

Note.—While working on the genus *Hesydrus*,

Table 1.—Eye measurements for species of *Trechalea*. Measurements are dimensions with outer limits of entities included. AE row = width of anterior eye row, PE row = width of posterior eye row, OQA = width of ocular quadrangle anteriorly or width of anterior median eyes, OQP = width of ocular quadrangle posteriorly or width of posterior median eyes, OQH = height of ocular quadrangle or height of anterior median eye and posterior median eye, PLE = diameter of posterior lateral eye, PME = diameter of posterior median eye, ALE = diameter of anterior lateral eye, AME = diameter of anterior median eye, PLE-PME = interdistance between posterior lateral eye and posterior median eye, PME-PME = interdistance between posterior median eyes, ALE-AME = interdistance between anterior lateral eye and anterior median eye, AME-AME = interdistance between anterior median eyes. lon = *T. longitarsis*, cez = *T. cezariana*, ama = *T. amazonica*, pau = *T. paucispina*, con = *T. connexa*, ext = *T. extensa*, ger = *T. gertschi*, mac = *T. macconnelli*, bol = *T. boliviensis*, lom = *T. lomalinda*, tri = *T. trinidadensis*. Measurements in millimeters.

Species/ sex	AE row	PE row	OQA	OQP	OQH	PLE	PME	ALE	AME	PLE-PME	PME-PME	ALE-AME	AME-AME
lon♂	1.88	3.56	1.08	1.78	1.70	0.76	0.74	0.32	0.49	0.58	0.27	0.15	0.25
lon♀	1.94	3.70	1.14	1.84	1.70	0.80	0.77	0.26	0.30	0.70	0.40	0.10	0.27
cez♂	1.99	3.70	1.16	1.78	1.60	0.88	0.76	0.32	0.51	0.67	0.35	0.12	0.27
cez♀	2.10	4.08	1.25	1.89	1.75	0.90	0.82	0.34	0.55	0.74	0.40	0.13	0.29
mac♂	2.08	3.78	1.22	1.88	1.80	0.86	0.80	0.35	0.60	0.62	0.41	0.14	0.28
mac♀	2.00	3.70	1.19	1.85	1.78	0.85	0.82	0.30	0.53	0.68	0.40	0.15	0.25
pau♂	1.79	3.29	1.09	1.60	1.48	0.70	0.70	0.29	0.49	0.56	0.40	0.10	0.23
pau♀	1.90	3.45	1.14	1.65	1.52	0.75	0.70	0.31	0.49	0.63	0.40	0.09	0.25
con♂	1.40	2.58	0.83	1.25	1.11	0.56	0.50	0.22	0.34	0.45	0.30	0.07	0.22
con♀	1.55	2.88	0.91	1.38	1.26	0.58	0.60	0.26	0.38	0.60	0.28	0.08	0.25
ext♂	1.71	3.25	1.01	1.61	1.42	0.78	0.70	0.28	0.40	0.50	0.32	0.10	0.23
ext♀	1.70	3.26	1.02	1.60	1.44	0.74	0.68	0.30	0.44	0.55	0.36	0.10	0.20
ger♂	1.48	2.80	0.85	1.32	1.15	0.55	0.50	0.25	0.34	0.52	0.30	0.09	0.21
ger♀	1.61	2.98	0.96	1.40	1.25	0.65	0.50	0.25	0.40	0.58	0.33	0.10	0.25
ama♂	1.35	2.45	0.83	1.27	1.10	0.55	0.50	0.19	0.33	0.43	0.30	0.10	0.19
ama♀	1.45	2.70	0.90	1.38	1.20	0.60	0.55	0.20	0.35	0.40	0.30	0.09	0.18
bol♂	1.07	2.13	0.57	1.15	0.94	0.47	0.48	0.18	0.23	0.32	0.27	0.08	0.16
bol♀	1.05	2.18	0.58	1.15	0.96	0.50	0.47	0.18	0.23	0.37	0.27	0.07	0.16
lom♂	1.27	2.44	0.72	1.27	1.12	0.55	0.54	0.20	0.28	0.38	0.30	0.10	0.23
lom♀	1.30	2.58	0.72	1.33	1.16	0.57	0.57	0.21	0.30	0.42	0.31	0.05	0.20
tri♀	1.03	2.05	0.65	1.05	0.91	0.45	0.45	0.16	0.27	0.37	0.22	0.05	0.15

I was impressed with its similarity with *Trechalea* and hold to the possiblity that later the two genera may be found to be congeneric. Currently, however, because of lack of sufficient males in *Hesydrus*, I will keep them as separate genera with the main distinction based on the flexible tarsi (i. e., flexible metatarsi only in *Hesydrus*) mentioned in the diagnosis above.

Trechalea longitarsis (C. L. Koch)
Figures 7, 11–15, 25; Map 1

Triclaria longitarsis C. L. Koch, 1848:65. (Holotype is a female from Colombia deposited in the Museum für Naturkunde der Humbolt-Universität, presumed lost. The Specimen #ZMB 2006, listed as the holotype, is misidentified and is not the original type specified by Koch [see discussion above]. A neotype male is hereby designated from Quebrada Docordo, ab. 110 km N of Palestina, Rio San Juan, Choco, Colombia, collected 20–25 January 1971 by B. Malkin and P. Burchard, deposited in the Field Museum of Natural History)

Trechalea longitarsis, Karsch, 1879:450. Roewer, 1954: 143. Bonnet, 1955-1959:4679.

Trechalea urinator Simon, 1898b:20. (Male and female syntypes from Guayaquil, Depto. Loja, Ecuador in the Muséum National d'Histoire Naturelle, examined.) Roewer, 1954:143; Bonnet, 1955–1959:4679. NEW SYNONYMY.

Diagnosis.—This is the only species of *Trechalea* with four retromarginal cheliceral teeth. Both sexes are also distinguished by the details of the genitalia. The median apophysis of the palpal bulb bears a distinct tubercle between the guide and ventral division (Figs. 11, 15), a feature shared only with *T. extensa* (Figs. 20, 53). *T. longitarsis* differs from the latter species by the

Table 2.—Leg measurements in male of *Trechalea longitarsis.*

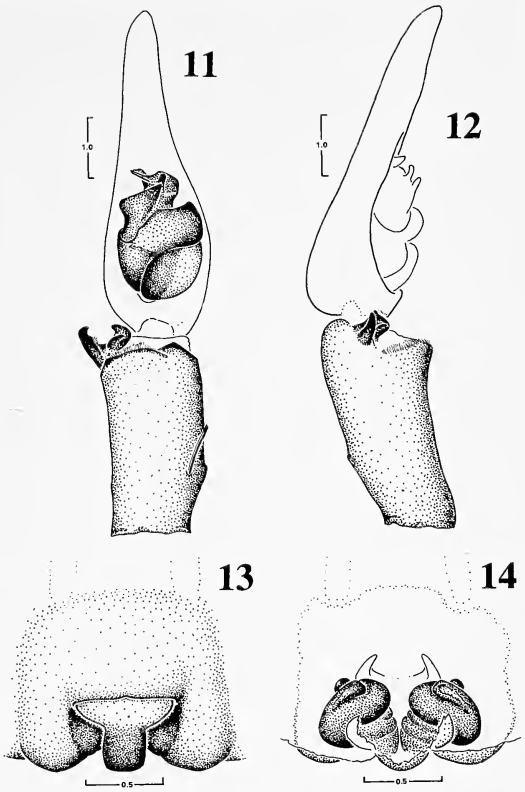
Leg segment	I	II	III	IV
Femur	18.5	21.2	16.0	21.0
Tibia-patella	25.2	26.6	20.0	25.4
Metatarsus	19.0	21.5	16.6	24.8
Tarsus	12.2	13.9	11.0	15.5
Total	74.9	83.2	63.6	86.7

length of the cymbium which is about twice the length of the bulb (Fig. 11).

Description.—*Male:* (Río San Juan, Depto. Choco, Colombia). Carapace low, cephalic area not elevated, length 11.1, width 9.5, medium brown with submarginal bands distinct posteriorly, less so anteriorly, dark at lateral margins and in eye region. Sternum light, unmarked, length 5.2, width 5.1; labium dark brown, lighter at distal margin, length 2.2, width 2.0. Clypeus height 1.36, width 5.0. Anterior eye row straight, a cluster of bristles posterior to each PLE, eye measurements in Table 1. Chelicerae face dark, clothed with light hairs mostly in proximal two-thirds, an oblique groove above fang and a longitudinal carina laterally on distal two-thirds, four retromarginal teeth equidistant, subequal in size except distal one slightly smaller. Legs IV-II-I-III, measurements in Table 2, ventral macrosetae pairs on tibiae are I-5, II-5, III-5, IV-5. Color of legs medium brown, unmarked. Abdomen length 9.5, hairy above, dark above and without distinct pattern except for reticulated and striated distribution of pigment, light ventrally.

Palpus (Figs. 11, 12), median apophysis (Fig. 15) with *ma* guide winged apically, and with a distinct distal tubercle situated between the dorsal and ventral subdivisions; cymbium length/palpal bulb length ratio 2.14. Tibial apophysis (Fig. 25) with *ecd* flattened and hooked distally and serrated along inner margin.

Female: (Río San Juan, Depto. Choco, Colombia). Carapace shape and color as in male, length 9.9, width 9.0. Sternum light, unmarked, length 5.8, width 5.2; labium color as in male, length 2.00, width 1.96. Clypeus height 1.41, width 5.15. Anterior eye row straight, eye measurements in Table 1. Chelicerae color and hair as in male. Legs IV-II-I-III, measurements in Table 3; ventral macrosetae pairs on tibiae I-5, II-4, III-4, IV-3. Color of legs as in male. Abdomen length 8.8, hairy above, color as in male except for indistinct pairs of light spots. Epigynum (Figs. 13, 14) with the lateral margins *mf* almost parallel; *s* mostly fused to *cd*.



Figures 11–14.—Genitalia of *Trechalea longitarsis* (Choco, Colombia): 11, 12, right palpus; 11, ventral view; 12, retrolateral view; 13, 14, epigynum; 13, ventral view; 14, dorsal view. Scales in mm.

Variation.—The average carapace length of eight males is 11.24 (range 10.8–11.8), and the average carapace length of nine females is 10.31 (range 9.5–11.0). The average cymbium/palpal bulb length ratio is 1.96 (range 1.81–2.19, n = 8).

Natural history.—Four egg sacs were found in three collections dated January, June, and October with an average diameter of 16.8 (range 15.0–19.8). All egg sacs were typically disc-shaped with both the top and bottom valves opaque and brown-colored. Two egg sacs were still attached to the spinnerets by threads. Apparently the principal habitat is around streams because most collection records refer to a river while one collection note stated explicitly, "near water". Another collection note stated, "en la selva".

Distribution.—From northern Peru northward to northern Colombia along the eastern river

Table 3.—Leg measurements in female of *Trechalea longitarsis.*

Leg segment	I	II	III	IV
Femur	18.3	20.5	16.0	20.6
Tibia-patella	23.2	25.6	18.5	23.6
Metatarsus	18.6	21.1	17.1	24.6
Tarsus	12.8	13.0	10.8	15.9
Total	72.9	80.2	62.4	84.7

drainages. There are no records of collections from the Amazon or Orinoco basins. (Map 1).

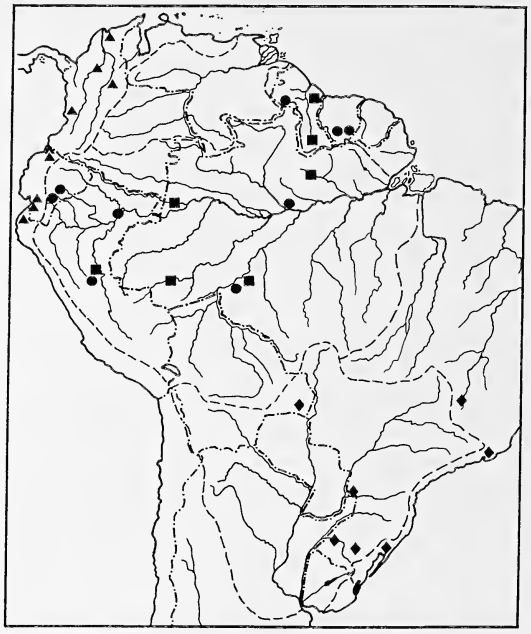
Specimens examined.—COLOMBIA: *Choco:* Quebrada Dorcordo, 110 km N of Palestina, Río San Juan, 20–25 Jan. 1971 (B. Malkin & P. Burchard), 5♂ 3♀ 5 juv. (FMNH); Pangola, 40 km N of Palestina, Río San Juan, 14–18 Jan. 1971 (B. Malkin & P. Burchard), 2♀, 6 juv. (FMNH); *Cauca:* Quebrada, Huangui, Río Saija area, 100 m (B. Malkin), 1♂ 2♀ 6 juv. (FMNH); *Magdalena:* Serr. Nueva Granada, Sierra Nevada de Santa Marta, 24 April 1975 (J. A. Kochalka), 1♂ 1♀ (JAK); *Santander:* Río Suarez, 800–1000 m, 11–17 Aug. 1946 (collector unknown), 2♂ 2 juv. (AMNH). **ECUADOR:** Pichincha: 12 km SW of Santo Domingo de los Colorados, 4–8 April 1971 (B. Malkin), 2♀ (FMNH); *El Oro:* Río Colorado Pasáje, 4 Nov. 1942 (Walls), 1 juv. (EXPE); *Imbabura:* Lita, Sept. 1984 (D. Bastidos), 1♂ (MECN); *Cañar:* Yanayacu, 22 Sept. 1984 (R. Navarrette), 1♀ (MECN). **PERU:** *Piura:* Caña Dulce, Oct. 1943 (C. & E. Ewing), 1♂ (CAS).

Trechalea cezariana Mello-Leitão
Figures 16, 26, 35–38; Map 1

Trechalea cezariana, Mello-Leitão, 1931:12, fig. 2 (The holotype is a female from Río Cruz, near Gramado, Municipio de Taquara, Est. Río Grando do Sul, Brazil, collected by Cezar Pinto, deposited in the Museo Nacional, Río de Janeiro, Brazil, examined.) Roewer, 1954:142; Bonnet, 1955–1959:4678.

Diagnosis.—The median apophysis of the palpus is notched anteriorly (Fig. 16) and the ectal division of the tibial apophysis is small, flat and curved (Fig. 26). The epigynum is characterized by the very wide and flattened middle field with a median groove (Fig. 37).

Description.—*Male:* (Lassance, Minas Gerais, Brazil). Carapace low, length 9.65, width 9.35, no distinct pattern, dark in eye region, a pair of small depressions with dark hairs anterior to thoracic groove; sternum light, unmarked, length 5.0, width 4.6; labium dark reddish brown, light distally, length 2.25, width 1.75. Clypeus height 1.14, width 4.25. Anterior eye row straight, eye measurements in Table 1. Chelicerae dark reddish brown, clothed with setae on anterior surface, oblique depression above fang, a longitudinal carina along distal third of anterolateral margin, three retromarginal teeth of equal size with gap between proximal two. Legs IV-II-I-III, light and unmarked, measurements in Table 4, ventral tibial spine pairs I-5, II-5, III-3, IV-4. Abdomen length, 8.0, marked with indistinct pattern above, light ventrally.



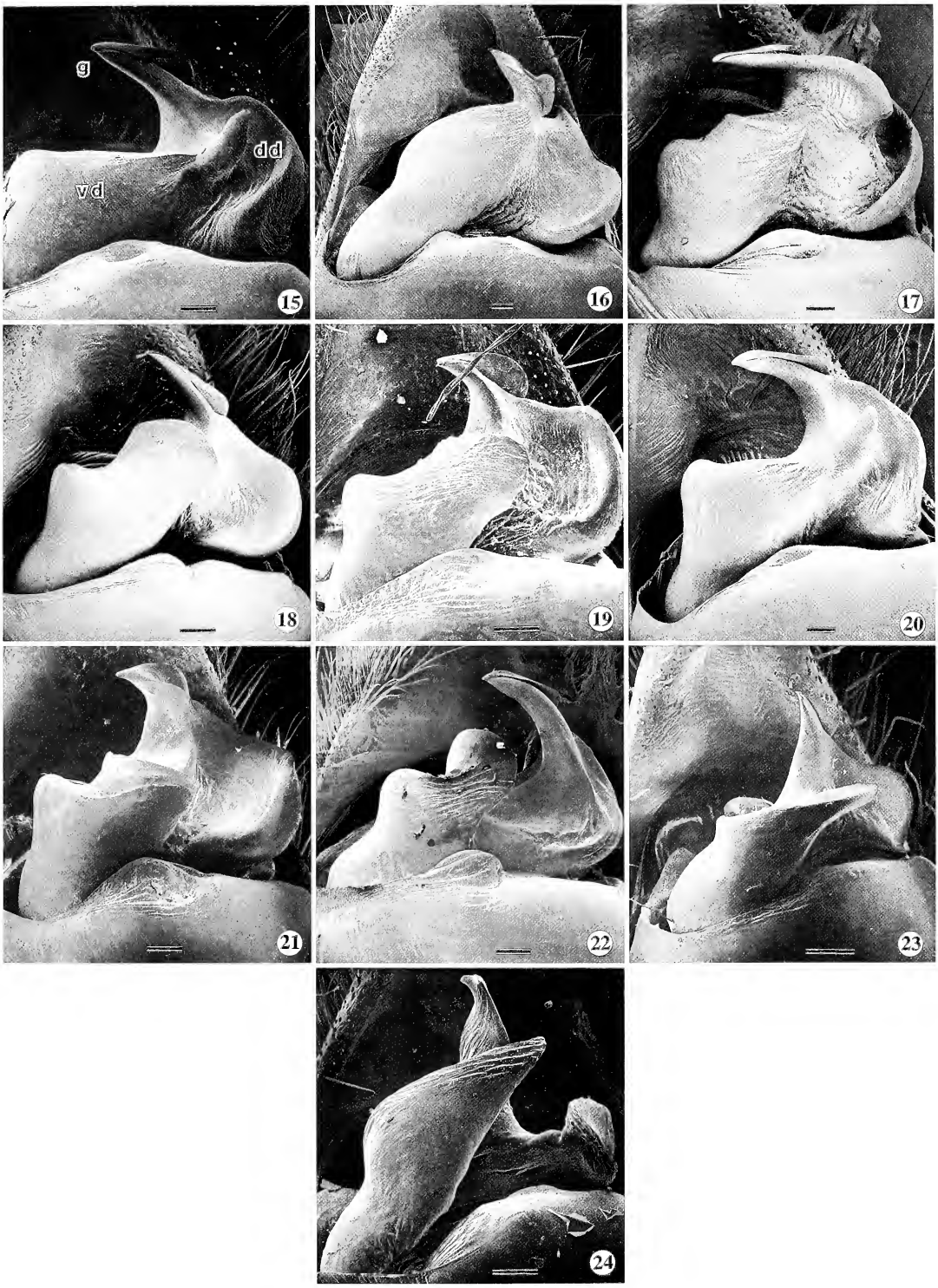
Map 1.—Distribution of species of *Trechalea* in South America. ● = *T. macconnelli*, ■ = *T. paucispina*, ◆ = *T. cezariana*, ▲ = *T. longitarsis*. Dashed lines indicate major river drainage basins and/or continental divides.

Palpus (Figs. 35, 36), *ma* (Fig. 16) notched, *rta* (Fig. 26) with *end* thickened and rounded, *ecd* small, thickened but acute distally and directed mediad.

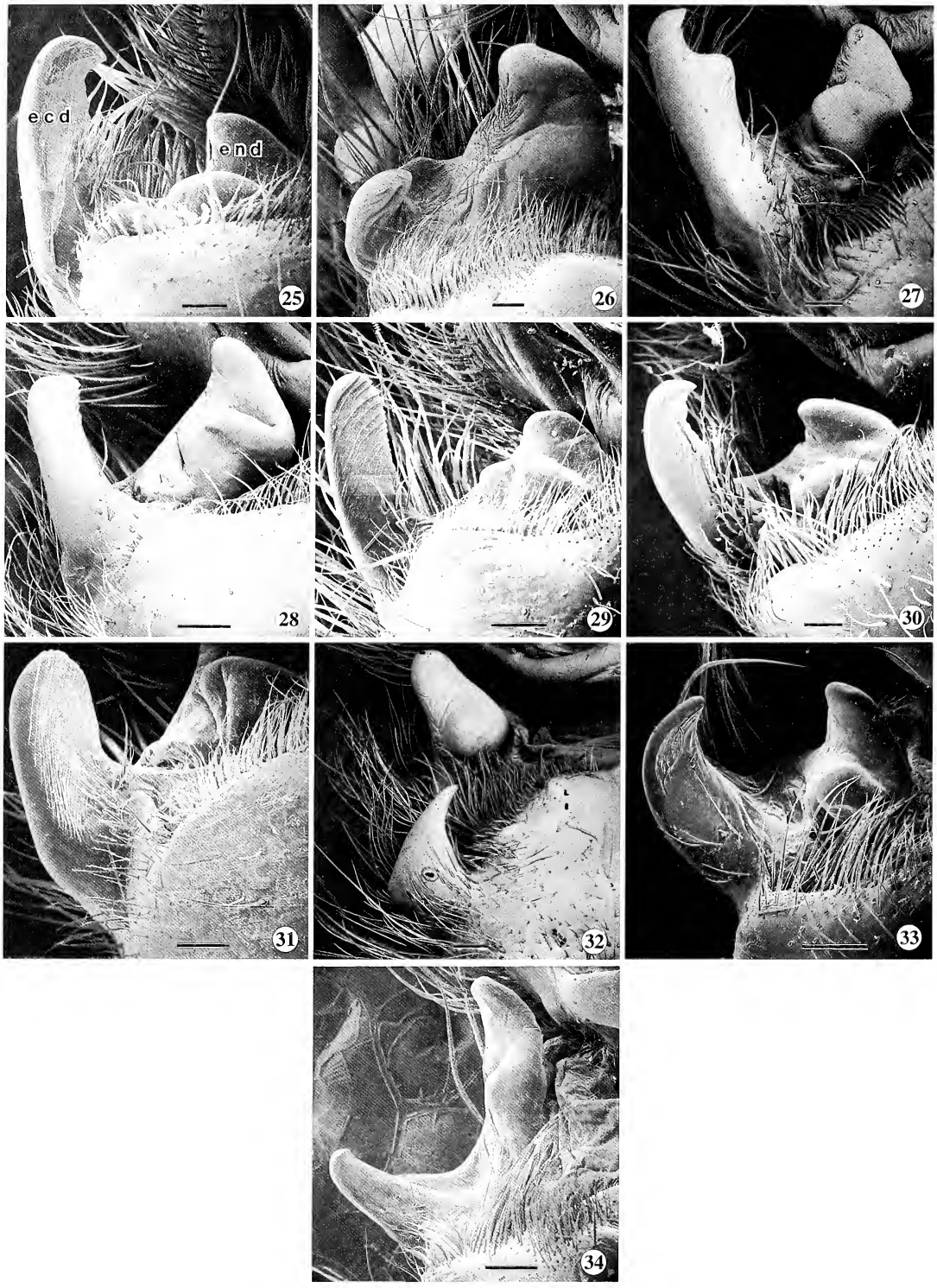
Female: (Lassance, Brazil). Carapace low, length 9.6, width 9.8 marked as in male; sternum

Table 4.—Leg measurements in male of *Trechalea cezariana.*

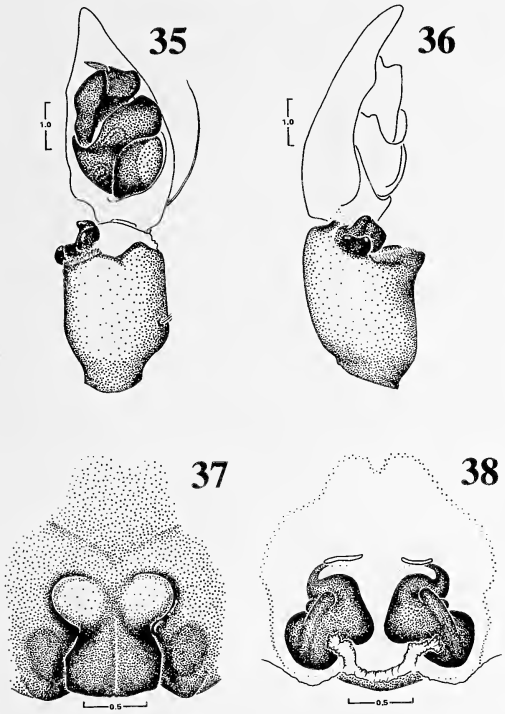
Leg segment	I	II	III	IV
Femur	14.1	16.6	13.8	16.4
Tibia-patella	19.3	22.0	16.6	20.3
Metatarsus	14.8	17.3	13.2	19.4
Tarsus	8.8	9.3	7.8	11.0
Total	57.0	65.2	51.4	67.1



Figures 15–24.—Scanning electron micrographs of median apophyses from right palps of species of *Trechalea*, ventral views; 15, *T. longitarsis* (dd = dorsal division, g = guide, vd = ventral division); 16, *T. cezariana*; 17, *T. macconnelli*; 18, *T. paucispina*; 19, *T. connexa*; 20, *T. extensa*; 21, *T. gertschi*, 22, *T. amazonica*; 23, *T. boliviensis*; 24, *T. lomalinda*. Scales: 100μ.



Figures 25–34.—Scanning electron micrographs of retrolateral tibial apophyses from right palps of species of *Trechalea*, ventral views: 25, *T. longitarsis* (ecd = ectal division, end = ental division); 26, *T. cezariana*; 27, *T. macconnelli*; 28, *T. paucispina*; 29, *T. connexa*; 30, *T. extensa*; 31, *T. gertschi*; 32, *T. amazonica*; 33, *T. boliviensis*; 34, *T. lomalinda*. Scales: 100μ.



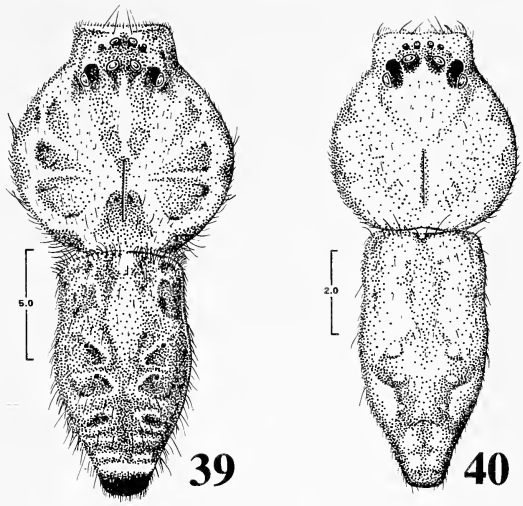
Figures 35–38.—Genitalia of *Trechalea cezariana* (Minas Gerais, Brazil): 35, 36, right palpus; 35, ventral view; 36, retrolateral view; 37, 38, epigynum; 37, ventral view; 38, dorsal view. Scales in mm.

light, unmarked, length 5.15, width 4.9; labium color as in male, length 1.35, width 1.8. Clypeus height 1.20, width 4.78. Anterior eye row straight, eye measurements in Table 1. Chelicerae as in male but without oblique depression, cheliceral teeth as in male. Legs IV-II-I-III, measurements in Table 5, light, unmarked ventrally but with faint oblique lateral gray maculae, pairs of macrosetae on venter of tibia I-4, II-4, III-4, IV-4. Abdomen length 12.25, marked with indistinct pattern above, light ventrally.

Epigynum (Figs. 37, 38) heavily sclerotized and dark, *mf* very wide, flattened with a median longitudinal groove; internal parts heavily sclerotized and fused together.

Table 5.—Leg measurements in female of *Trechalea cezariana.*

Leg segment	I	II	III	IV
Femur	13.5	15.8	13.2	15.7
Tibia-patella	18.5	21.7	16.5	19.7
Metatarsus	13.6	16.0	13.3	18.8
Tarsus	8.3	9.3	8.0	11.2
Total	53.9	62.8	51.0	65.4



Figures 39, 40.—Dorsal patterns of species of *Trechalea*: 39, *T. macconnelli*; 40, *T. boliviensis*. Scales in mm.

Variation.—The average carapace length of six males is 10.02 (range 8.3–11.0) and the average carapace length of seven females is 9.66 (range 8.1–10.3).

Natural history.—None of the collection records provide information about the type of habitat. Two quite flat egg sacs of typical construction were found with females collected 25 March and 4 October and were 19.25 and 18.5 respectively.

Distribution.—The rather sparse number of collections of this species indicate that the main area of distribution is in the various tributaries of the Río de la Plata in southern Brazil. There are additional records from the coastal areas of Brazil in the states of Río Grande do Sul and Río de Janeiro, and a single collection from the upper tributary of Río São Francisco in the state of Minas Gerais. (Map 1).

Specimens examined.—**BRAZIL:** *Minas Gerais:* São Gonçalo das Tobacas, Lassance, 25 March 1925 (D. M. Cochran), 2♂ 3♀, 3 imms. (USNM); Río de Janeiro, Thayer Expedition, 1♂ (MCZ); *Río Grande do Sul:* Reserva Biológica do Ibicui-Mirim, Santa María, 4 Oct. 1989 (N. Silveira), 1♀ (MCN), Itaúba, Arroio do Tigre, 7 April 1978 (A. A. Lise), 2♂ (MCN), 11 April 1978 (H. Bischoff), 1♀ (MCN), 11 April 1978 (A. A. Lise), 1♂ 1♀ (MCN). **ARGENTINA:** *Misiones:* Parque Nacional Iguazu, Sept. 1963 (M. E. Galiano), 1♂ 1♀ (MEG). **BOLIVIA:** *Santa Cruz:* Estación el Portón, Serrania de Santiago, 24 Sept. 1955 (F. Azambuya), 1♂ (CAS).

Table 6.—Leg measurements in male of *Trechalea macconnelli.*

Leg segment	I	II	III	IV
Femur	20.4	22.3	16.6	21.0
Tibia-patella	25.3	26.8	19.0	25.2
Metatarsus	19.5	21.8	16.1	24.3
Tarsus	12.5	13.6	11.2	16.0
Total	77.7	84.5	62.9	86.5

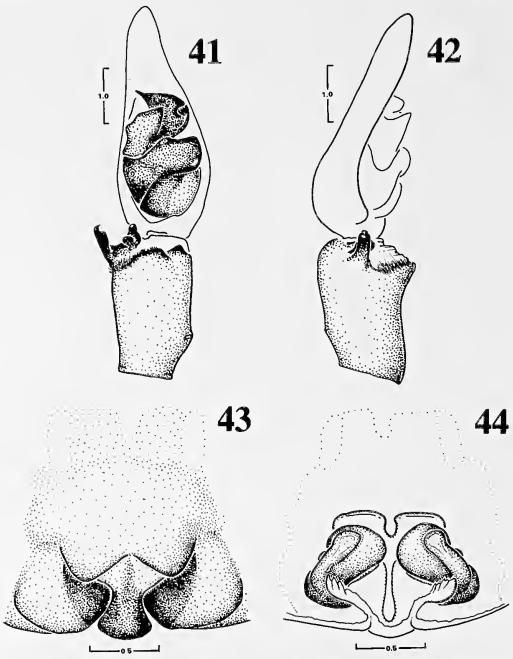
Trechalea macconnelli Pocock
Figures 17, 27, 39, 41–44; Map 1

Trechalea macconnelli Pocock 1900:67, 68, fig. 2e (The holotype is a male from Mount Roraima [base 3500 feet] Guyana, collected by F. V. McConnell and J. J. Quelch, deposited in The Natural History Museum, London, examined). F. Pick.-Cambridge, 1903: 159, 163. Petrunkevitch, 1911:548. Roewer, 1954: 143. Bonnet 1955–1959:4679.

Trechalea ellacombei F. Pickard-Cambridge 1903:161, 162, pl. XV, fig. 6 (The holotype is a female from Bergen-Dal, Surinam, collected May 1892 by E. W. Ellacombe, deposited in The Natural History Museum, London, examined). Petrunkevitch 1911:548. Roewer 1954:142. Bonnet 1955-1959:4679. NEW SYNONYMY.

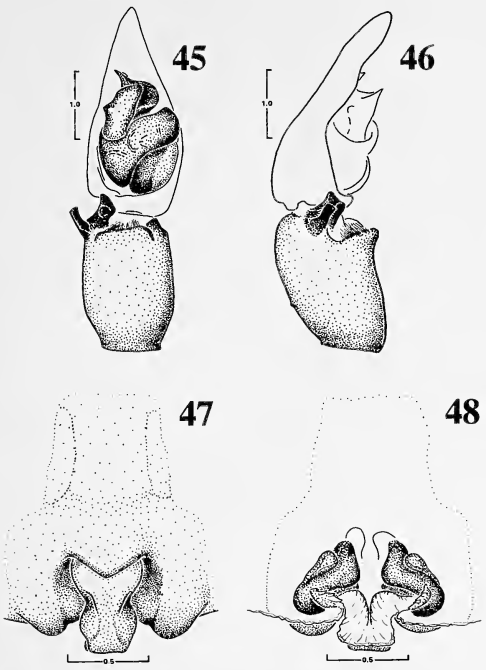
Diagnosis.—Both sexes are distinguished by the transverse band of white hairs dorsally near the posterior apex of the abdomen (Fig. 39). The males are also distinguished by the shape of the median apophysis (Fig. 17) and the hook-like configuration of the ectal division of the tibial apophysis (Fig. 27). Both sexes have a distinct black tip on the dorsal abdominal apex (Fig. 39).

Description.—*Male:* (Cusuimi, Pastaza, Ecuador). Carapace low, cephalic area somewhat elevated, length 10.7, width 10.0, medium brown, darker at margin and black in eye region, light hairs on clypeus; sternum light, unmarked, length 5.4, width 5.2; labium dark brown, lighter distally, length 2.15, width 1.92. Clypeus height 1.20, width 3.8. Anterior eye row straight, eye measurements in Table 1. Chelicerae face dark, clothed with light hairs clustered in longitudinal patches, an oblique groove above each fang and a short longitudinal carina laterally, three retromarginal teeth equal in size with distal two closer together. Legs IV-II-I-III, measurements in Table 6, ventral macrosetae pairs on tibiae are I-5, II-5, III-4, IV-4. Color of legs generally medium brown, lighter on ventral side of femora and without distinct pattern. Abdomen length 9.0, hairy above with reticulated pattern of dark pigment except with a medium light cardiac area, a transverse light band near the posterior apex and a patch of dark hairs apically; light ventrally. Palpus (Figs. 41, 42, second male from same locality), *g* of *ma* (Fig. 17) divided into two blade-like carinae and rugose on some surfaces; *ecd* of *rta* (Fig. 27) flattened and hooked at tip.



Figures 41–44.—Genitalia of *Trechalea macconnelli*: 41, 42, right palpus (Pastaza, Ecuador); 41, ventral view; 42, retrolateral view; 43, 44, epigynum (Rondônia, Brazil); 43, ventral view; 44, dorsal view. Scales in mm.

Female: (Jamari, Rondônia, Brazil). Carapace shape as in male, light submarginal bands and radiating light lines on darker background (Fig. 39), dark around eye region, length 9.7, width 9.6; sternum light, unmarked, length 5.2, width 4.9; labium color as in male, length 2.05, width 1.80. Clypeus height 1.15, width 4.40. Anterior eye row straight, eye measurements in Table 1. Chelicerae face dark, clothed with light hairs clustered into longitudinal patches with long dark hairs between. Legs II-IV-I-III, measurements in Table 7, ventral macrosetae pairs on tibiae I-5, II-5, III-4, IV-4. Color of legs generally dark with distinct but irregular pattern particularly on prolateral surfaces. Abdomen length 10.8, hairy above especially laterally, bold pattern (Fig. 39) of light and dark including a transverse band of light hairs near apex, apex with a dense patch of black hairs; light ventrally. Epigynum (Figs. 43,



Figures 45–48.—Genitalia of *Trechalea paucispina* (Guyana): 45, 46, right palpus; 45, ventral view; 46, retrolateral view; 47, 48, epigynum; 47, ventral view; 48, dorsal view. Scales in mm.

44) with the *mf* dark and narrowed in the center; *s* mostly fused to *cd*.

Variation.—A considerable range of dorsal patterns occurs from a bold pattern of light and dark marks to a more uniform dark color with only the subapical light transverse band present. Correspondingly, the pattern on the legs varies from a uniform color to a bolder pattern. Two lobes of the *pma* of the epigynum may be enlarged (Fig. 43) or inconspicuous.

These are rather large spiders with the average carapace length of 12 males of 9.65 (range 8.5–10.8) and mean carapace length of nine females of 9.3 (range 8.0–10.0).

Natural history.—Egg sacs were found with collections from Brazil (November, 15.3 diam.) and Peru (June, 24.0 diam.). A note with a male from Ecuador reads: "Spiders under bridge on surface or under water on vertical rock surfaces."

Distribution.—Found in the upper Amazon River basin in eastern Ecuador, northeastern Peru, and in Brazil from the State of Rondônia northward and including the high altitude drainages of coastal rivers in southern Surinam and western Guyana. (Map 1).

Table 7.—Leg measurements in female of *Trechalea macconnelli*.

Leg segment	I	II	III	IV
Femur	17.1	18.7	12.7	17.0
Tibia-patella	22.2	23.7	15.8	20.2
Metatarsus	16.2	17.7	13.9	18.7
Tarsus	10.4	11.9	8.5	11.5
Total	65.9	72.0	50.9	67.4

Specimens examined.—**BRAZIL:** *Amazônas:* Manaus, Reserva Ducke, on side of swimming pool, 30 Mar. 1986 (J. Adis), 2♂ (INPA); *Rondônia:* Porto Vieho, Río Jamari, 27 Dec. 1988 (Equipe Operação Jamari), 1♂ (MCN); 18 Nov. 1988 (Equipe Operação Jamari), 8♀ 1 juv. (MCN). **ECUADOR:** *Pastaza:* Cusuimi, on Río Cusuimi, 320 m, 1–5 June 1971 (B. Malkin), 2♂ (FMNH); Cusuimi, on Río Cusuimi, 150 km SE of Puyo, 15–22 May 1971 (B. Malkin), 1♂ 2♀ 1 juv. (FMNH); *Morona-Santiago:* Yanzatza, 33.4 km N, El Pincho, 820 m (J. A. Anderson), 1♂ (USNM). **PERU:** *Loreto:* Río Yarapa, 80 km S Iquitos, June 1986 (J. & K. Ribardo), 1♀ (CAS); Río Ampiacu, 13 Nov.–19 Dec. 1961 (B. Malkin), 1♀ 1 juv. (AMNH); Aquaitia, 170 m, 1–2 Sept. 1946 (F. Woytowski), 1♀ 1 juv. (AMNH); *Huanuco:* Tingo María, 670 m (Weyrauch), 1♂ (CAS); Tingo María, 43 mi. E (E. I. Schlinger & E. S. Ross), 1♂ (CAS). **SURINAM:** Berg-en-del [dal?], May 1892 (E. W. Ellacombe), 1♀ (holotype of *T. ellacombei* F. Pick.-Camb.)(BMNH); Litani, Fetibreek, 15 Sept. 1939 (Gercher), 1♂ (USNM); Keyserberg airstrip, E of Zuid River (no date) (H. Baetty), 1♀ (FMNH).

Trechalea paucispina Caporiacco
Figures 18, 28, 45–48; Map 1

Trechalea paucispina Caporiacco, 1947:22 (The holotype is a female from Presso, Great Falls, Demerda, Guyana, collected September 1931 by Beccari and Romiti, deposited in the Museo Zoologico della Specola, Firenze, Italy, examined). Caporiacco, 1948: 633, figs. 24–26. Roewer, 1954:143.

Diagnosis.—Both sexes are distinguished by details of their genitalia. The palpal bulb has a distinctive shape of the median apophysis guide distally (Fig. 18), and the tibial apophysis ectal division truncated apically (Fig. 28). The epigynum externally has the middle field flared along the middle of its length over medial projections from lateral lobes and the posterior margin of the anterior field projecting posteriorly (Fig. 47).

Description.—*Male:* (Canje Ikuruwa River, Guyana). Carapace low, cephalic area somewhat elevated, length 8.0, width 7.5, medium brown medially with distinct submarginal bands, dark at lateral margins and in eye region. Sternum

Table 8.—Leg measurements in male of *Trechalea paucispina.*

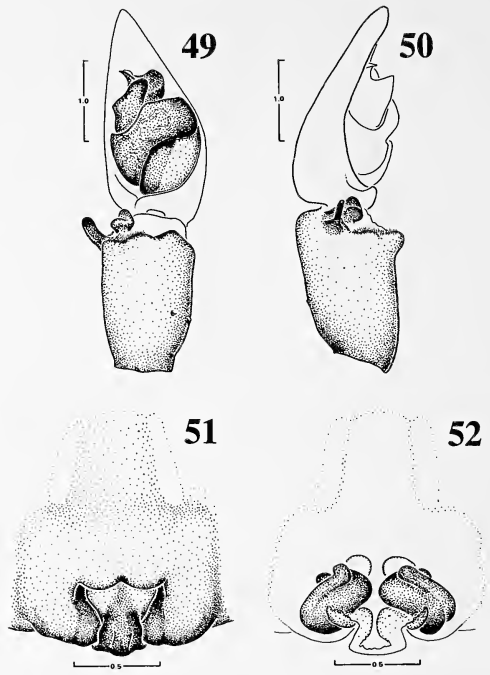
Leg segment	I	II	III	IV
Femur	13.3	14.2	11.3	14.7
Tibia-patella	16.9	18.1	13.2	17.2
Metatarsus	13.2	14.2	10.8	16.1
Tarsus	8.5	8.9	7.5	10.3
Total	51.9	55.4	42.8	58.3

light, unmarked, length 4.1, width 3.8; labium dark brown, darker laterally at basal half, lighter at distal margin, length 1.65, width 1.38. Clypeus height 0.78, width 3.70. Anterior eye row straight, a cluster of bristles posterior to each PLE, eye measurements in Table 1. Chelicerae face dark, clothed with light hairs and longer more erect dark hairs, an oblique groove above fang and a short longitudinal carina laterally, three retromarginal teeth equal in size with distal two slightly closer together. Legs IV-II-I-III, measurements in Table 8, ventral macrosetae pairs on tibiae are I-4, II-5, III-4, IV-3. Color of legs generally light with distinct markings on prolateral surfaces of all femora and tibiae-patellae. Abdomen length 7.3, hairy above with a distinct pattern including transverse marks in the posterior third, light ventrally. Palpus (Figs. 45, 46), *ma* (Fig. 18) with *g* winged apically, *rta* (Fig. 28) with *ecd* straight, truncated apically.

Female: (Canje Ikuruwa River, Guyana). Carapace shape and color as in male, length 8.2, width 8.2. Sternum light, unmarked, length 4.3, width, 4.0; labium color as in male, length 1.76, width 1.48. Clypeus height 0.80, width 4.05. Anterior eye row straight, eye measurements in Table 1. Chelicerae face dark, clothed with light hairs and scattered longer more erect dark hairs. Legs IV-II-I-III, measurements in Table 9, ventral macrosetae pairs on tibiae I-4, II-4, III-3, IV-3. Color of legs as in male. Abdomen length 9.5, hairy above, color as in male. Epigynum (Figs. 47, 48) with the *mf* narrowed centrally and flared laterally over *ll* and the *pma* projecting posteriorly; *s* mostly fused to *cd*.

Variation.—Of eight females measured, the average carapace length is 8.1 (range 7.4–9.2). The only male available had the carapace length of 8.0.

Natural history.—Most collection labels indicate that the specimens were taken from rivers, however a collection from Guyana also includes the notation; "forest savanna". Three egg sacs found with females average 17.3 (13.7–24.0) and are of the typical trechaleid structure.



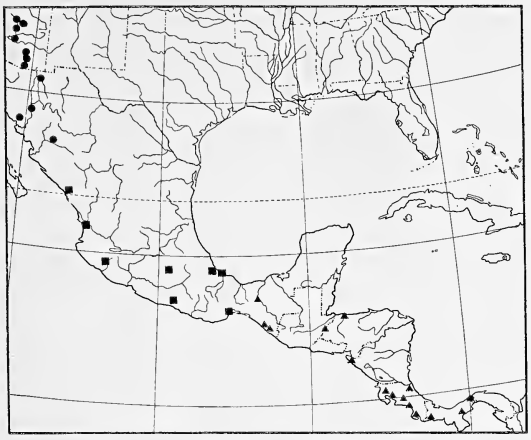
Figures 49–52.—Genitalia of *Trechalea connexa*: 49, 50, right palpus (Veracruz, Mexico); 49, ventral view; 50, retrolateral view; 51, 52, epigynum (Morelos, Mexico); 51, ventral view; 52, dorsal view. Scales in mm.

Distribution.—Amazon River tributaries in northwestern Brazil and central Peru northward into the coastal river drainages of Guyana. (Map 1).

Specimens examined.—**GUYANA:** Canje Ikuruwa River, 57.50W:5.70N, Aug.-Dec. 1961 (G. Bently), 1♂ 2♀ (AMNH); Shudicar River, upper Essequibo River, 1 Jan. 1938 (W. G. Hassler), 1♀ (AMNH). **PERU:** *Loreto:* Aquaitia [Aguaytia R.], 170 m, 1–2 Sept. 1946 (F. Woytkowski), 1♀ (AMNH). **BRAZIL:** *Amazônas:* Ica (Thayer Expedition), 1♀ (MCZ); *Rondônia:* Jamari, #18568, 18 Nov. 1988 (Equipe Operação Jamari), 1♀ (MCN); *Acrê:* Río Purus NW of Sena Madureira Seringal Santo Antonio (above Manuel Urbano), 15–18

Table 9.—Leg measurements in female of *Trechalea paucispina.*

Leg segment	I	II	III	IV
Femur	12.6	13.8	11.0	14.3
Tibia-patella	16.3	17.3	13.0	17.3
Metatarsus	11.8	12.8	10.4	15.9
Tarsus	7.6	8.3	7.3	10.0
Total	48.3	52.2	41.7	57.5



Map 2.—Distribution of species of *Trechalea* in USA, Mexico and Central America. ● = *T. gertschi*, ■ = *T. connexa*, ▲ = *T. extensa*.

Sept. 1973 (B. Patterson), 1♀ (MCZ); *Pará:* Río Maputra [Río Mapuera?] 10 mi. S of Equator, 8–9 Feb. 1938 (W. G. Hassler), 1♀ (AMNH).

Trechalea connexa (O. Pickard-Cambridge)
Figures 19, 29, 49–52; Map 2

Triclaria connexa O. Pick.-Camb., 1898:233 (The holotype is a male from Atoyác, Veracruz, Mexico, collected by H. H. Smith, deposited in The Natural History Museum, London, examined).

Trechalea connexa, F. O. Pick.-Camb., 1902:312, 313. Petrunkevitch, 1911:548. Roewer, 1954:142. Bonnet, 1955–1959:4679.

Diagnosis.—Both sexes are distinguished by details of their genitalia. The median apophysis (Fig. 19) differs from *T. gertschi* in details of the guide and ventral division. The retrolateral tibial apophysis also resembles that of *T. gertschi* but is thinner (Fig. 29). In the female, the middle field is narrowed centrally but is flared distally (Fig. 51) while the same structure in *T. gertschi* is broad throughout without distinct central narrowing.

Description.—*Male:* (Fortín, Veracruz, Mexico). Carapace low, cephalic area not elevated, length 6.5, width 6.2, medium brown with indistinct light areas laterally, dark at margin and in eye region; sternum light, unmarked, length 3.5, width 3.3; labium dark brown, lighter distally, an irregular, longitudinal furrow at the basal half on each side. Clypeus height 0.67, width 3.00. Anterior eye row straight, eye measurements in Table 1. Chelicerae face medium brown, smooth, almost glabrous medially with hairs peripherally, an oblique groove above each fang

Table 10.—Leg measurements in male of *Trechalea connexa.*

Leg segment	I	II	III	IV
Femur	9.5	11.0	9.1	10.7
Tibia-patella	12.5	14.0	10.9	13.2
Metatarsus	9.7	6.3	9.0	12.4
Tarsus	5.6	6.1	5.3	7.2
Total	37.3	37.4	34.3	43.5

and a longitudinal carina laterally on distal one-third of its length, three retromarginal teeth equal in size and equidistant. Legs IV-(II-I)-III, measurements in Table 10, ventral macrosetae pairs on tibiae are I-4, II-4, III-4, IV-4. Color of legs generally light with a faint pattern on prolateral surface of femora and tibiae. Abdomen length 6.1, hairy above with reticulated pattern of dark pigment, darker posteriorly and with light spots anteriorly around muscle attachments and around anterior margin; light ventrally. Palpus (Figs. 49, 50), *ma* (Fig. 19) with *g* winged apically; *rta* (Fig. 29) with *ecd* flattened, rounded apically.

Female: (Cuernavaca, Morelos, Mexico). Carapace shape and color as in male, length 7.2, width 7.0; sternum light, unmarked, length 3.5 width 3.6; labium color as in male, length 1.45, width 1.25. Clypeus height 0.75, width 3.36. Anterior eye row straight, eye measurements in Table 1. Chelicerae face dark, clothed with scattered short, light hairs and scattered, longer, more erect hairs. Legs IV-II-I-III, measurements in Table 11, ventral macrosetae pairs on tibia are I-4, II-4, III-3, IV-3. Color of legs as in male. Abdomen length 8.0, hairy above, pattern in poor condition but similar to male. Epigynum (Figs. 51, 52) with *mf* flared and grooved posteriorly; *s* mostly fused to *cd*.

Variation.—In alcohol, the dorsum shows a radiating group of dark lines on the carapace with vague evidence of irregular submarginal bands, while the abdomen is generally dark with varying light marks near the anterior margin including the cardiac area, and around the abdominal muscle apodemes. The average carapace lengths of 14 males is 7.45 (range = 6.1–9.3) and of 25 females is 7.63 (range 6.4–9.25).

Natural history.—Little biological data are contained with the specimens and are limited to two references to the vicinity of water. Egg sacs are in four collections which are 12.7, 14.5, 10.8, and 17.8 diameter from April, June, July, and August respectively.

Table 11.—Leg measurements in female of *Trechalea connexa.*

Leg segment	I	II	III	IV
Femur	9.3	10.9	9.4	10.6
Tibia-patella	12.5	13.1	11.4	14.3
Metatarsus	8.9	10.2	8.9	11.7
Tarsus	5.5	6.0	5.5	6.7
Total	36.2	40.2	35.2	43.3

Distribution.—From the Isthmus of Tehuantepec of Mexico northwestward through central Veracruz on the Atlantic coast to southern Jalisco on the Pacific coast. (Map 2).

Specimens examined.—MEXICO: *Veracruz:* Fortín, 28 April-1 May 1944 (C. Bolivar & I. Piña), 2♂ (AMNH); *Oaxaca:* Tehuantepec, 22 Dec. 1947 (T. McDougall), 1♂ (AMNH); *Morales:* Cuernavaca, 1 April 1942, 1♀ (AMNH); *Guerrero:* Colotlipa, Río Blanco, 1 Aug. 1941, 1♀ (AMNH); *Jalisco:* 5 mi. N Pihuamo 2350 ft., 5 Aug. 1967 (R. E. Leech), 1♀ (REL); *Sinaloa:* Camino Real de Piaxtla, 4 May 1949 (G. W. Bradt), 3♀ (AMNH); *Nayarit:* Tepic, 2 Aug. 1947 (C. Goodnight), 1♀ (AMNH), 2–7 Aug. 1947 (C. & M. Goodnight & B. Malkin), 5 mi. NW Tepic, 13 May 1963 (W. J. Gertsch & W. Ivie), 5♂ 3♀ 2 juv. (AMNH), Mecatan 800 ft., 2 May 1949 (G. M. Bradt), 1♂ 2♀ 1 juv. (AMNH), Jesus María, 25 June 1955 (B. Malkin), 4♂ 8♀ (AMNH), 1–15 July 1955 (B. Malkin), 1♂ 3♀ (AMNH), 22–30 June 1955 (B. Malkin), 1♂ (AMNH), July 1955 (B. Malkin), 1♀ (AMNH), Arroyo Santiago, 3 mi. NW Jesus María, 4-6 July 1955 (B. Malkin), 1♀ (AMNH), 4 July 1955 (B. Malkin), 1♀ (AMNH).

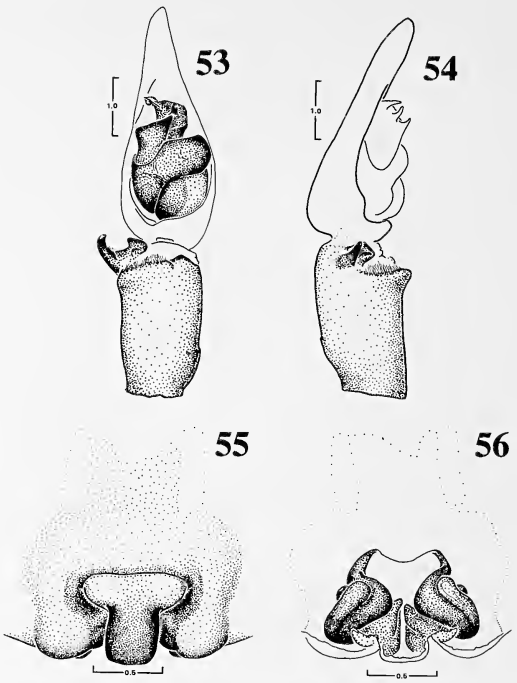
Trechalea extensa (O. Pickard-Cambridge)
Figures 20, 30, 53–56; Map 2

Triclaria extensa O. Pickard-Cambridge, 1896, 1:174–175 (The holotype is a male from Rokminhí, Guatemala, collected by Sarg, deposited in The Natural History Museum, London, examined).

Trechalea extensa, F. Pickard-Cambridge 1902, 2:313. Petrunkevitch, 1911:549. Roewer, 1954, 2a:143. Bonnet, 1955–1959:4679.

Trechalea magnifica Petrunkevitch, 1925:169–170 (The syntypes are from Wilcox dam on San Lorenzo River, Bocas Del Monte, La Mesa and Santiago, Panama, deposited in the Museum of Comparative Zoology, examined). Roewer, 1954:143. Bonnet, 1955–1959:4679. NEW SYNONYMY.

Diagnosis.—Both sexes are distinguished from other species by details of the genitalia. The median apophysis of the male palpal bulb bears a distinct tubercle between the guide and ventral division (Fig. 20), a feature shared only with *T. longitarsis* (Fig. 15). *Trechalea extensa* differs from the latter species by the length of the cymbium which is distinctly less than half the length of the bulb (Fig. 53). The middle field of the epigynum is short and usually with the sides almost parallel (Fig. 55). See diagnosis of *T. longitarsis* for other comparisons.



Figures 53–56.—Genitalia of *Trechalea extensa* (Canal region, Panama): 53, 54, right palpus; 53, ventral view; 54, retrolateral view; 55, 56, epigynum; 55, ventral view; 56, dorsal view. Scales in mm.

Description.—*Male:* (Barro Colorado Island, Lago Gatún, Panama). Carapace low, cephalic area not elevated, length 8.8, width 8.1, light brown background color with lighter submarginal bands more distinct posteriorly, dark at lateral margins, in eye region and a spot on each side of clypeus. Sternum light, unmarked, length 4.5, width 4.3; labium dark brown, lighter at distal margin, length 1.80, width 1.62. Clypeus height 1.05, width 4.08. Anterior eye row straight, a cluster of bristles posterior to each PLE, eye measurements in Table 1. Chelicerae face dark, clothed with light hairs mostly in proximal two-thirds, an oblique groove above fang and a longitudinal carina laterally on distal half, three retromarginal teeth of equal size with distal two closer together. Legs II-IV-I-III, measurements in Table 12, ventral macrosetae pairs on tibiae I-4, II-4, III-3, III-3. Color of legs generally light except for distinct dark marks on prolateral sur-

Table 12.—Leg measurements in male of *Trechalea extensa.*

Leg segment	I	II	III	IV
Femur	14.3	16.2	12.5	16.1
Tibia-patella	19.4	20.4	14.7	19.7
Metatarsus	15.1	17.1	12.4	15.3
Tarsus	10.0	11.0	8.3	12.4
Total	58.8	64.7	48.0	63.5

Table 13.—Leg measurements in female of *Trechalea extensa.*

Leg segment	I	II	III	IV
Femur	13.1	15.0	11.9	15.3
Tibia-patella	17.2	19.0	13.9	18.7
Metatarsus	12.9	14.6	11.4	18.1
Tarsus	8.0	9.1	7.6	10.0
Total	51.2	57.7	44.8	62.1

face of all legs. Abdomen length 9.2, hairy above, color a reticulated pattern of dark pigment with distinct small, scattered, dark spots, and lighter in cardiac area and a pair of indistinct spots in the posterior third, light ventrally. Palpus (Figs. 53, 54), *ma* (Fig. 20) with *g* winged apically, and with distinct distal tubercle situated between *g* and *vd*; cymbium/palpal bulb length ratio 1.67. The *rta* (Fig. 30) with *ecd* flattened and hooked distally and serrated along inner margin.

Female: (Barro Colorado Island, Lake Gatún, Panama). Carapace shape and color as in male but with markings more distinct, length 8.8, width 8.5. Sternum light, unmarked, length 4.5, width 4.3; labium color as in male, length 1.74, width 1.52. Clypeus height 1.06, width 4.00. Anterior eye row straight, eye measurements in Table 1. Chelicerae color, teeth, and hair as in male but with the addition of longer and more erect hairs grouped mostly in longitudinal rows. Legs IV-II-I-III, measurements in Table 13, ventral macrosetae pairs on tibiae I-5, II-4, III-4, IV-4. Color of legs as in male. Abdomen length 11.6, color and hair as in male. Epigynum (Figs. 55, 56), *mf* sides almost parallel; *s* mostly fused to *cd*.

Variation.—The average carapace length of 19 males is 9.05 (range 8.3–10.0), and the average carapace length of 32 females is 9.38 (range 8.2–12.0). The average cymbium length/palpal bulb length ratio of 19 males is 1.72 (range 1.60–1.88). The width of the middle field of the epigynum is wider in specimens in the northern part of the range.

The retromarginal cheliceral teeth number is typically three, but two males from Panama had four on only one side. One specimen had the fourth a full-sized tooth while the second had only a tiny added tooth at the base of another tooth.

Natural history.—These spiders are a distinctive feature of the streams of Panama and Costa Rica. They seem to be completely restricted to the stream margins and bases of emergent rocks and debris. They have been collected from large, open-canopied rocky streams and from first-order streams in vegetational thickets. They bite readily the collector's hand. Van Berkum (1982) has reported an apparent preference for shrimps as prey in Rincón de Osa in Panama.

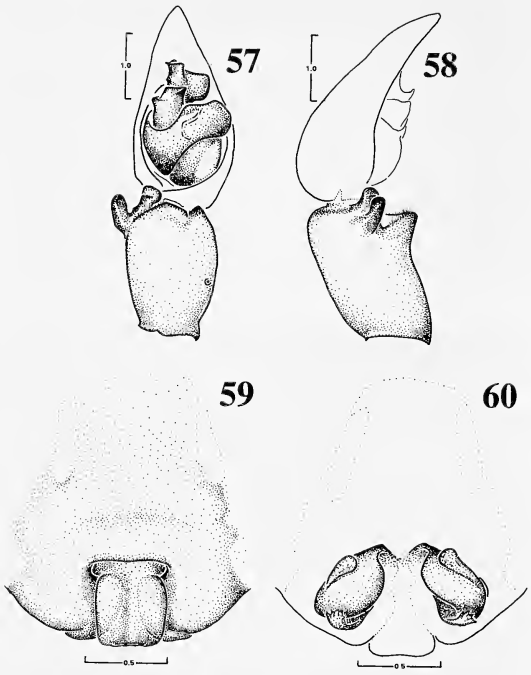
Egg sacs are in five collections; the average of four is 13.9 (range 10.0–15.5) collected during the months of May and June.

Distribution.—In Central America ranging from Central Panama in the south to the Mexican state of Chiapas in the north. (Map 2).

Specimens examined.—**PANAMA:** (Central area around Canal, summary of several collections), 5♂ 13♀, several juv.; El Valle de Anton, 1 April 1945 (C. D. Michener), 1♂, 1♀ (AMNH); El Valle, July 1936 (A. M. Chickering), 1♀ (MCZ); river 10 km W of David, 8 Aug. 1983 (Carico, Coyle, Eberhard, Coddington), 9♂ 2♀ several juv. (JEC). **COSTA RICA:** river 5.3 km N of Las Cañas on Rt. #19, 11 Aug. 1983 (Carico, Coyle, Vogel), 2♂ 1♀ (JEC); San Antonio de Escazú, near San José, 14 Aug. 1983 (J. E. Carico), 1♀ (JEC), May 1984 (W. Eberhard), 1♀ (MCZ); Puntarenas, Esterillos, 20 June 1970 (D. C. Robinson & R. Saeña), 1♀ (MZUCR); 18 km S of San Isidro del General, 2–3 June 1972 (J. Baldridge), 1♀ (MZUCR); Butler's Finca 9°18′: 83°o47′W, 28 Jan. 1976 (Roth-Schroepfer), 1♀ (AMNH); Los Diamantes, Guapiles (C. E. Valerio), 1♀ (MZUCR); San Mateo (N. Banks), 1♀ (MCZ); Tilarán (C. E. Valerio), 1♂ (MZUCR). **HONDURAS:** Copán (R. V. Chamberlin), 2♀ 5 juv. (AMNH), Lancetilla, July 1929 (A. M. Chickering), 3♀ 3 juv. (MCZ). **MEXICO:** *Chiapas:* 5.6 mi. SE Chiapa de Corzo, 2500 ft., 16 Aug. 1966 (D. E. Breedlove & J. Emmel), 1♀ (CAS), Mapastepec, June-July, 1940 (H. Wagner), 1♀ (AMNH), Rancho la Esperanza, 40 km Escuintla, 22 Jan. 1945 (T. C. Schneirla), 1♀ (CAS). **NICARAGUA:** Polvón (McNeill), 1♂ 2♀ (MCZ).

Trechalea gertschi Carico & Minch
Figures 21, 31, 57–60; Map 2

Trechalea gertschi Carico & Minch, 1981:154-156, figs. 1–4 (Male holotype from 9 mi. S of Sunflower, Maricopa County, Arizona, USA, collected by E. Minch,



Figures 57–60.—Genitalia of *Trechalea gertschi* (Arizona, USA): 57, 58, right palpus; 57, ventral view; 58, retrolateral view; 59, 60, epigynum; 59, ventral view; 60, dorsal view. Scales in mm.

9 June 1979, deposited in the American Museum of Natural History, examined). Brignoli, 1983:700. Platnick, 1989:389.

Diagnosis.—In the male, the median apophysis has the ventral division truncated apically and a notch retrolaterally (Fig. 21). The ectal division of the retrolateral tibial apophysis is a rounded projection flattened ventrally and often with a serrated surface (Fig. 31). The median field of the epigynum is flattened and overlapping the lateral lobes (Fig. 59).

Description.—*Male:* (Holotype). Carapace length 7.0, width 7.4., moderately low with ocular area dark, marginal band dusky, serrated submarginal light band, median light band extending from thoracic groove to posterior margin of carapace. Sternum light, unmarked, length 3.6, width 3.8; labium dark, with transverse groove, length 1.6, width 1.4. Clypeus height 0.75, width 3.60. Anterior eye row slightly recurved, eye measurements in Table 1. Chelicerae face dark with three equal sized retromarginal teeth, distal two closer. Legs IV-II-I-III, measurements in Table 14, ventral macrosetae pairs on tibiae are I-4, II-4, III-3, IV-3. Color of legs light with faint band on dorsal side of femora, patellae-tibiae.

Table 14.—Leg measurements in male of *Trechalea gertschi.*

Leg segment	I	II	III	IV
Femur	10.0	12.0	9.6	11.2
Tibia-patella	13.4	15.5	11.6	14.2
Metatarsus	10.0	11.8	9.4	13.5
Tarsus	5.5	6.5	5.5	7.6
Total	38.9	45.8	36.1	46.5

Abdomen length 6.0, dorsum has irregular darker mottling clothed with several black, long setae, venter light and unmarked except for black setae in genital area. Palpus (Figs. 57, 58), *ma* (Fig. 21) with *g* winged on either side, *vd* truncated distally with retrolateral notch and transverse grooves, *rta* (Fig. 31) with *ecd* with uniform width, rounded apically, ventral side flattened with serrated surface. (Figs. 21, 31 from another male from type locality).

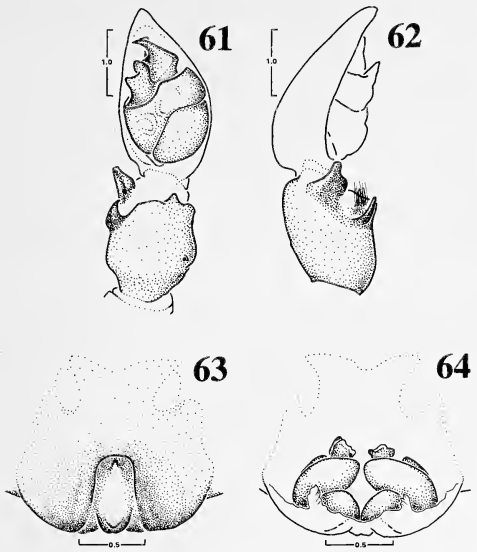
Female: (Paratype). Carapace shape and color as in male, length 7.9, width 7.4. Sternum light, unmarked, length 4.0, width 4.0.; labium similar to male, length 1.60, width 1.50. Clypeus height 0.80, width 3.70. Anterior eye row straight, eye measurements in Table 1. Chelicerae as in male. Legs IV-II-III-I(?), measurements in Table 15, ventral macrosetae pairs on tibiae I-4, II-2, III-3, IV-3. Color of legs as in male. Abdomen length 8.5, color pattern as in male. Epigynum (Figs. 59, 60) has the *mf* broad with an anterior constriction and overlapping *ll* posteriorly.

Variation.—The average carapace length of 20 males is 7.59 (range 6.8–8.4), and the average carapace length of 21 females is 7.57 (range 6.8–8.9).

Natural history.—All instars of individuals are found restricted to the margins of apparently permanent streams within the xeric regions. Typically they are found on the surfaces of rocks and pebbles of varying sizes near the water margin. They readily run across water and occasionally crawl underwater by walking down the surface

Table 15.—Leg measurements in female of *Trechalea gertschi.*

Leg segment	I	II	III	IV
Femur	10.5	12.5	11.0	12.5
Tibia-patella	13.9	16.5	13.3	14.6
Metatarsus	10.0	12.2	10.7	14.7
Tarsus	6.2	—	6.1	8.1
Total	40.6	—	41.1	49.9



Figures 61–64.—Genitalia of *Trechalea amazonica* (Amazônas, Brazil): 61, 62, right palpus; 61, ventral view; 62, retrolateral view; 63, 64, epigynum; 63, ventral view; 64, dorsal view. Scales in mm.

of a partly submerged rock. Females carry egg sacs by the spinnerets and show other typical trechaleid behavior described above.

Five egg sacs were found with the collections. Their dates and sizes (stated only if in a condition to measure) are: 25–27 June (3 egg sacs, 18.8 & 19 mm), 6 July (1 egg sac, 15 mm), 17 July (2 egg sacs). Two apparently gravid females were in collections made in January and July.

Distribution.—From Yavapai County of central Arizona, USA southward into the Mexican states of Sonora and Chihuahua. (Map 2).

Material examined.—**USA:** *Arizona:* Maricopa County, 9 mi. S Sunflower, 3 June 1979, (E. Minch), 1♂ 2♀, (AMNH), 11 July 1979, (E. Minch), 2♂, (AMNH); Yavapai County, Clear Cr., 11 mi. E Camp Verde, 25–27 June 1986, (J. E. Carico), 4♀, (JEC); Pinal County, Sycamore Cr. 30 mi. NE Apache Junction, 28 June 1986, (J. E. & E. L. Carico, E. Minch), 3♂ 1♀, (JEC); Pima County., Sabino Canyon, Santa Catalina Mts. nr. Tuscon, 1 Sept. 1939, (R. H. Crandall), 1♂ 1♀, (AMNH), 5 Oct. 1937, (Crandall), 1♂, (AMNH), 6 July 1939, (R. A. Flock), 1♀, (MCZ), 17 July 1971, (J. E. Carico), 3♂ 6♀, (AMNH); Santa Cruz County, Santa Rita Mts., 1♀, (AMNH); Gila County, Gisela, 5 Nov. 1977, (E. Minch), 1♂, (AMNH). **MEXICO:** *Sonora:* 6 mi. E Alamos, Río Cuchujachi, 22 June 1966, (V. Roth) 6♂ 3♀ (AMNH); SE Alamos on Río Cuchujaqui, Jan. 1968, (V. Roth), 1♂ 3♀, (AMNH); 57 mi. SE Aqua Prieta on bank of Río El Batista [Bavispe], 26 June 1972, (G. Dingerkus), 1♀, (AMNH); *Chihuahua:* Urique Río, 21 April 1986, (V. D. Roth), 1♂, (JEC).

Table 16.—Leg measurements in male of *Trechalea amazonica.*

Leg segment	I	II	III	IV
Femur	8.9	9.0	7.5	9.7
Tibia-patella	11.3	10.9	8.5	10.8
Metatarsus	7.7	7.8	6.8	10.4
Tarsus	4.5	4.7	4.5	6.0
Total	32.4	32.4	27.3	36.9

Trechalea amazonica F. O. Pickard-Cambridge
Figures 22, 32, 61–64; Map 3

Trechalea amazonica F. O. Pickard-Cambridge, 1903: 163, plate 15, figs. 18–20 (The holotype is a male from Santarem, Amazônia, Brazil, collected by F. O. Pickard-Cambridge 1895–1896, deposited in The Natural History Museum, London, examined; two female paratypes with holotype from the same locality).

Trechalea manauensis Carico, in Carico et al., 1985, 6(7):289–294, figs. 1–4 (The holotype is a male from Ihla de Marchantaria, Río Solimões (near Manaus), Amazônas, Brazil, collected by J. Adis, 28 June 1981, deposited in the Systematic Entomology collection of Instituto de Pesquisas da Amazônia, examined; female paratype from the same locality). Platnick, 1989:398. NEW SYNONYMY.

Diagnosis.—The palpal bulb is distinguished by the blade-like and dual rounded edge of the median apophysis ventral division (Fig. 22) and the relative size and shape of the components of the retrolateral tibial apophysis (Fig. 32). The epigynum is distinguished by the shape of the middle field (Fig. 63) and unique shape of the internal components (Fig. 64).

Description.—*Male:* (Holotype of *T. manauensis*). Carapace length 5.5, width 5.3, moderately low, light colored with indistinct markings and ocular area dark. Sternum light, unmarked, length 2.80, width 0.98; labium dark especially laterally, lighter at anterior margin, length 1.18, width 0.98. Clypeus height 0.60, width 2.70. Anterior eye row straight, eye measurements in Table 1. Chelicerae face swollen, dark, clothed with light hairs, an oblique groove above fang and a longitudinal carina laterally on distal one-half, three equal-sized retromarginal teeth with distal two closest. Legs IV-(I-II)-III, measurements in Table 16, ventral macrosetae pairs on tibiae are I-4, II-5, III-3, VI-3. Color of legs light with faint bands on dorsal side of fem-

Table 17.—Leg measurements in female of *Trechalea amazonica.*

Leg segment	I	II	III	IV
Femur	8.7	8.7	7.5	9.7
Tibia-patella	10.7	10.8	8.3	11.2
Metatarsus	7.1	7.4	6.9	10.3
Tarsus	3.5	4.4	4.3	6.0
Total	30.0	31.3	27.0	37.2

ora, patellae-tibiae, and metatarsus. Abdomen length 6.1, dorsum color a reticulated gray background, three pairs of diagonal gray maculae, numerous erect, dark setae anteriorly, venter unmarked on light background. Palpus (Figs. 61, 62), *ma* (Fig. 22) with *vd* flattened with two rounded projections and *g* tapered and curved at tip, *rta* (Fig. 32) with *end* large and pointed distally, *ecd* smaller, tapered, curved, acute with brush of long hairs separating the two divisions.

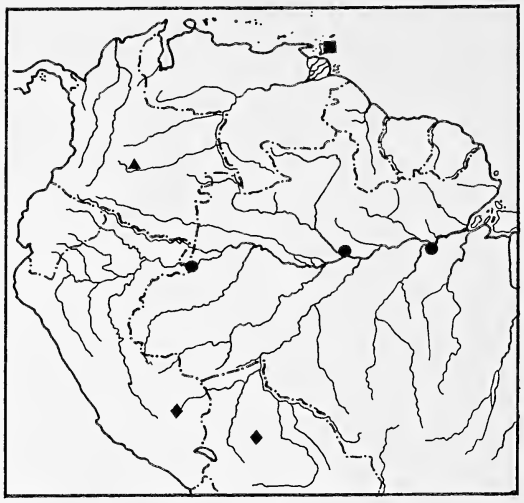
Female: (Paratype of *T. manauensis*). Carapace length 5.7, width 5.5, shape and color as in male. Sternum light, unmarked, length 2.95, width 2.75; labium similar to male, length 1.20, width 1.05. Clypeus height 0.57, width 2.80. Anterior eye row straight, eye measurements in Table 1. Chelicerae dark, clothed with light hairs, teeth as in male. Legs IV-(I-II)-III, measurements in Table 17, ventral macrosetae pairs on tibiae I-4, II-4, III-3, IV-3. Color of legs as in male. Abdomen length 7.0, color patterns as in male. Epigynum (Figs. 63, 64), *pma* extending posteriorly around *mf* to form U-shaped frame around *mf*. The posterior apex of the *mf* is black and somewhat set off from the light-colored anterior portion by a constriction.

Variation.—Average carapace length of six males is 5.45 (range 4.65–5.75) and average carapace length of 11 females is 5.9 (range 5.4–6.8).

Natural history.—Adis and Penny (in Carico et al. 1986) provide much detailed information on the natural history, behavior, and parasitism on this species which inhabits the inundation forests of the central Amazon River area. Six egg sacs were found in the collections; February (12.0 diam.), 31 March (3 egg sacs, 8.35, 8.5, 8.5), 28 April (9.6, [infested with chalcid wasps]), 31 May (9.8).

Distribution.—Known only from the main channel, Río Solimões and Río Amazônas in the state of Amazônas, Brazil. (Map 3).

Material examined.—**BRAZIL:** *Amazônas:* Ihla Marchantara, Solimões, 28 April 1981 (J. Adis), 3♂ 1♀, 16 Dec. 1987 (E. H. Buckup), 1♂, Río Solimões in *várzea* forest 15 km from Manaus, 31 March 1976 (J. Adis), 3♂ 4♀, Lago Janauacá nr. Río Solimões, 50 km from Manaus, no date (J. Adis), 3♀, Río Taruma Mirîam, 20 km upstream from Manaus, 28 April 1976 (J. Adis), 1♀, (same locality), 31 May 1976 (J. Adis), 1♀, (previous specimens deposited variously in INPA, AMNH, JEC).



Map 3.—Distribution of species of *Trechalea* in northern South America. ▲ = *T. lomalinda*, ■ = *T. trinidadensis*, ● = *T. amazonica*, ◆ = *T. boliviensis.*

Trechalea boliviensis, new species
Figures 23, 33, 40, 65–68; Map 3

Type.—The holotype is a male from Bolivia, Dpto. Beni, Est. Biol. Beni, Zone 1, ca. 4°47′S: 66°15′W, ca. 225 m; collected 8–14 November 1989, by Coddington, Larcher, Penaranda, Griswold, and Silva, deposited in the Instituto de Ecología, La Paz, Bolivia. Female paratype from the type locality deposited in the United States National Museum.

Etymology.—The name means "from Bolivia," the country of origin.

Diagnosis.—Both sexes are distinguished from those of all other species by the narrowed shape of the posterior third of the abdomen (Fig. 40), a patch of black hairs on the posterior apex of the abdomen, and details of the shape of their respective genitalia (Figs. 23, 33, 67, 68).

Description.—*Male:* (Holotype). Carapace low, cephalic area elevated, length 4.2, width 4.4, generally light but with dark on margin and black around each eye; sternum light, unmarked, length 2.55, width 2.4; labium dark, light at distal margin, with a longitudinal darker band in the basal

Table 18.—Leg measurements in male of *Trechalea boliviensis.*

Leg segment	I	II	III	IV
Femur	8.8	8.3	6.4	9.0
Tibia-patella	11.7	10.0	6.9	9.7
Metatarsus	8.6	7.6	5.9	9.9
Tarsus	5.3	5.0	4.1	6.1
Total	34.4	30.9	23.3	34.7

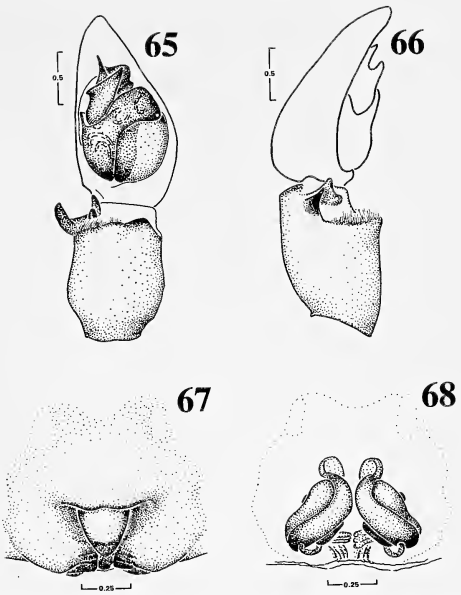
half on each side, length 0.88, width 0.72. Clypeus height 0.50, width 2.20. Anterior eye row straight, eye measurements in Table 1. Chelicerae face dark, basal segments clothed with light hair and a few larger, more erect dark bristles medially, oblique depression above fang, and longitudinal carina on distal one-third of lateral margin; three retromarginal teeth equal in size with distal two closer together. Legs IV-I-II-III, measurements in Table 18, ventral macrosetae pairs on tibiae are I-6, II-6, III-4, IV-4; color light ventrally with indistinct markings on other surfaces. Abdomen length 5.5, median cleft at anterior margin, narrowed posteriorly, irregular dark band laterally, irregular dorsal pattern (Fig. 40), light ventrally, patch of dark hairs at posterior apex. Palpus (Figs. 65, 66), *ma* (Fig. 23) with *g* acute and curved ventrally; *rta* (Fig. 33) with *ecd* with three lobes and *ecd* blade-like and slightly curved medially.

Female: (Paratype). Carapace shape and color as in male, length 4.5; width 4.5; sternum light, unmarked, length 2.75, width 2.35; labium as in male, length 0.98, width 0.80. Clypeus height 0.50, width 1.3. Anterior eye row straight, eye measurements in Table 1. Chelicerae face generally dark, darker distally, basal segments clothed with light hair and several more erect dark bristles, teeth as in male. Legs IV-I-II-III, measurements in Table 19, ventral macrosetae pairs on tibia I-6, II-6, III-4, IV-4; color as in male. Abdomen length 5.5, color as in male.

Epigynum (Figs. 67, 68) with *mf* triangular, light anteriorly, with dark and narrowed posterior apex; *s* fused to *cd* except distally, *ll* wrinkled posteriorly.

Variation.- Carapace length average of four males is 3.91 (range 3.7–4.2) and the two females have carapace lengths of 4.2 and 4.5.

Specimens examined and distribution.—BOLIVIA: *Beni:* (Type collection), 2♂ 2♀ (USNM). **PERU:** *Cuzco:* Quincemil, 750 m, August 1962 (Peña), 2♂ (MCZ). (Map 3).



Figures 65–68.—Genitalia of *Trechalea boliviensis* (Beni, Bolivia): 65, 66, right palpus; 65, ventral view; 66, retrolateral view; 67, 68, epigynum; 67, ventral view; 68, dorsal view. Scales in mm.

Trechalea lomalinda, new species
Figures 24, 34, 69–72; Map 3

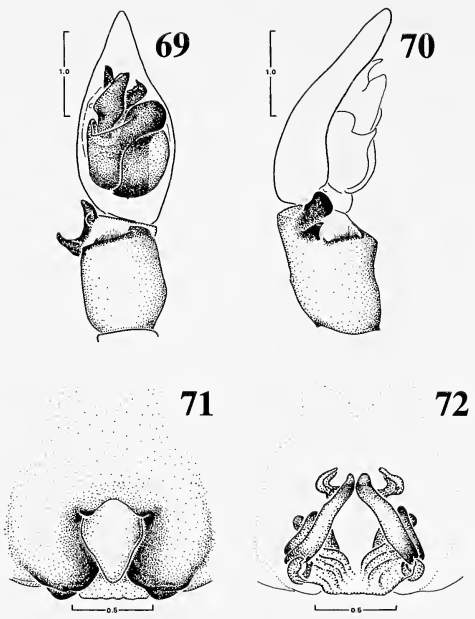
Type.—The holotype is a male from Lomalinda, Puerto Lleras, Meta, Colombia, 300 m elevation, collected 15 April 1986 by B. T. Carroll, deposited in the California Academy of Sciences Museum. Paratype female from the type locality, collected March 1987 by B. T. Carrol, deposited in the California Academy of Sciences Museum.

Etymology.—The name is a noun in apposition taken from the name of the type locality.

Diagnosis.—The ental division of male retrolateral tibial apophysis is more prominent than ectal division (Fig. 34). The dorsal division of the median apophysis has a unique prominent projection other than the guide (Fig. 24). In the female epigynum the middle field is triangular and entirely white (Fig. 71); the copulatory duct is distinctively narrow (Fig. 72).

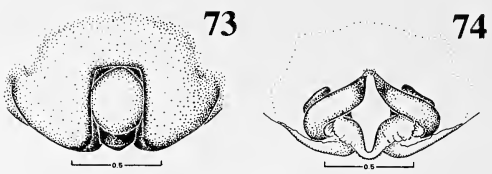
The first leg pair is longer than the second. The leg femora are slender and distinctly tapered.

Description.—*Male:* (Holotype). Carapace very low, cephalic area elevated, length 5.75, width 5.3, no distinct pattern and without black in the ocular area; sternum light, unmarked, length 3.1, width 2.7; labium dark reddish brown, light at distal margin, length 1.2, width 1.06. Clypeus height 0.70, width 2.87. Anterior eye row straight,



Figures 69–72.—Genitalia of *Trechalea lomalinda* (Meta, Colombia): 69, 70, right palpus; 69, ventral view; 70, retrolateral view; 71, 72, epigynum; 71, ventral view; 72, dorsal view. Scales in mm.

eye measurements in Table 1. Chelicerae face dark, clothed with conspicuous light hair proximally, and clothed sparsely distally with fine hairs, oblique depression above fang, and longitudinal carina on lateral margin; three retromarginal teeth equidistant and equal in size. Legs IV-I-II-III, measurements in Table 20, ventral macrosetae pairs on tibiae are I-6, II-6, III-4, IV-4, color light ventrally with indistinct markings on other surfaces except for two oblique marks on the distal part of prolateral surface of femur III and a longitudinal mark on prolateral surface of patella III. Abdomen length 5.1, shrivelled and without apparent pattern. Palpus (Figs. 69, 70), *ma* (Fig. 24) with *dd* with a prominent projection besides the *g*. The *vd* relatively large and acute and hooked distally. The *rta* (Fig. 34) with



Figures 73, 74.—Epigynum of *Trechalea trinidadensis* (Trinidad): 73, ventral view; 74, dorsal view. Scales in mm.

end relatively prominent, flattened and rounded apically, *ect* directed laterad with acute tip turned mediad.

Female: (Paratype). Carapace shape as in male, indistinct light pattern on lighter background, dark at edge especially at edge of cephalic area, and dark in eye region, length 6.0, width 5.7; sternum light unmarked, length 3.15, width 2.8; labium color as in male, length 1.25, width 1.10. Clypeus height 0.73, width 3.0. Anterior eye row straight, eye measurements in Table 1. Chelicerae face dark, clothed with conspicuous light hair proximally, and clothed sparsely distally with fine hair on a glossy integument; teeth as in male. Legs IV-I-II-III, measurements in Table 21, ventral macrosetae pairs on tibiae are I-5, II-5, III-3, IV-3; dark pattern on legs most distinct on prolateral surfaces and missing from ventral surface of femora. Abdomen length 7.3, light ventrally, color dorsally composed of reticulated pattern of dark changing to fine lines posteriorly and laterally, light spots around muscle apodeme marks. Epigynum (Figs. 71, 72) with *mf* very light and triangular, *s* mostly fused to *cd*; *cd* narrow.

Variation.—The average carapace length of six males is 5.36 (range 5.0–5.75). The carapace lengths of two females are 5.9 and 6.0.

Natural history.—A note with one of the collections states: "grasslands; patches of jungle, woods, marsh. Indoors, daylight."

Specimens examined and distribution.—Known only from Colombia, Depto. Meta, Pto. Lleras, Lomalinda

Table 19.—Leg measurements in female of *Trechalea boliviensis.*

Leg segment	I	II	III	IV
Femur	7.6	7.3	6.0	8.1
Tibia-patella	9.7	8.7	6.5	8.7
Metatarsus	6.4	6.0	5.3	8.5
Tarsus	4.0	4.2	4.1	5.6
Total	27.7	26.2	21.9	30.9

Table 20.—Leg measurements in male of *Trechalea lomalinda.*

Leg segment	I	II	III	IV
Femur	10.3	9.6	7.9	11.0
Tibia-patella	13.9	12.2	8.9	11.9
Metatarsus	9.9	9.0	7.4	11.5
Tarsus	6.1	6.0	5.8	7.9
Total	40.2	36.8	30.0	42.3

Table 21.—Leg measurements in female of *Trechalea lomalinda.*

Leg segment	I	II	III	IV
Femur	9.6	9.8	8.1	10.8
Tibia-patella	12.3	11.7	9.0	11.9
Metatarsus	8.5	8.3	7.3	11.6
Tarsus	5.3	5.8	5.9	7.6
Total	35.7	35.6	30.3	41.9

(73°22′W:3°18′N), 300 m, from three collections by B. T. Carroll: 15 April 1986 (holotype) (CAS); March 1989, 1♀ (CAS); 7 March 1986, 5♂ 2♀ 1 juv. (JEC). (Map 3).

Trechalea trinidadensis, new species
Figures 73, 74; Map 3

Type.—The holotype is an adult female from Port-of-Spain, Trinidad, collected by Erik N. Kjellesvig-Waering on 28 May 1968, deposited in the American Museum of Natural History.

Etymology.—The name means "from Trinidad" taken from the name of the type locality.

Diagnosis.—This species is characterized by the unique long spines on the pedipalps, the spination pattern on the ventral side of the tibiae and details of the genitalia (Figs. 73, 74).

Description.—*Female:* (Holotype). Carapace moderately low, length 4.0, width 3.8, pattern obscured with light marginal area evident, black around each eye but none coalescing; sternum light, unmarked, length 2.05, width 2.00; labium moderately dark, light on apical margin, length 0.87, width 0.77. Clypeus height 0.41, width 1.90. Anterior row straight, eye measurements in Table 1. Chelicerae moderately dark, rubbed of setation, three retromarginal teeth, equidistant, proximal one smallest, distal two equal in size. Legs IV-II-I-III, ventral macrosetae pairs on tibiae are I-5, II-5, III-3, IV-2; measurements in Table 22, no pattern discernible. Pedipalp with macrosetae longer than tibiae. Abdomen length 5.1, marked with a distinct but irregular pattern dorsally, light ventrally. Epigynum (Figs. 73, 74) with the *pma* extending around the *mf* to form a squared U-shaped rim; the *mf* pale and bulbous anteriad, narrowed and dark posteriad.

Table 22.—Leg measurements in female of *Trechalea trinidadensis.*

Leg segment	I	II	III	IV
Femur	6.0	6.1	5.1	7.0
Tibia-patella	7.6	7.5	5.9	7.7
Metatarsus	5.2	5.4	4.8	7.5
Tarsus	3.2	3.5	3.5	4.5
Total	22.0	22.5	19.3	26.7

Specimens examined and distribution.—Known only by the single type specimen. (Map 3).

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RESEARCH NOTE

COHABITATION AND COPULATION IN *IXEUTICUS MARTIUS* (ARANEAE, AMAUROBIIDAE)

Ixeuticus martius (Simon 1899) is a solitary, medium size cribellate spider. In spite of its very high abundance its biology is poorly known. However, I observed some cases of coexistence and tolerance between males and juvenile females for this species in the field. Male–juvenile female cohabitation has been long known in the Gnaphosidae and Clubionidae (Bristowe 1941), and it has shown to be common in the Salticidae and Araneidae (Jackson 1986). Austad (1984) and Jackson (1986) analysed this phenomenon and suggested it is a mating tactic among spiders. There are few reports on sexual behavior in the Amaurobiidae: precopulatory communication (Krafft 1978; Leborgne 1984), copulation (Gerhardt 1923, 1924; Gregg 1961), and cohabitation (Jackson 1986). I therefore thought it was important to communicate my observations on cohabitation and copulation in this Neotropical spider species.

Three male–subadult female pairs were observed cohabiting in their webs during 1989: pair 1 in Marindia, Canelones (December 2) and pairs 2 and 3 in Prado, Montevideo (both December 8). The web of pair 2 was contiguous with another web which contained another subadult female; the male was twice seen passing from one web to the other. No attacks were seen, but another smaller male was observed in the periphery of both webs. With the exception of this male, all individuals were captured and observed under laboratory conditions. During observations of copulation the room temperature was 27° C and relative humidity 61%.

Both spiders of pair 2 remained in contact inside the refuge built by the female in the lab. Five days after capture, at 1230 h (counted as minute zero of the observation), the female molted during a period of 11.4 min. At 23 min, the male repeatedly tapped the female and the nearby exuvia, and placed himself in various positions in relation to the female (ventral–ventral, face to face, etc.). Finally, the male placed himself on the female's side, both with the ventral zone upwards (Fig. 1). Palpal insertions started at 44.8 min, while the male vibrated his abdomen sagittally. The copulatory pattern was as follows: insertion with one palp—palpal withdrawal, and chewing-like movements on it—new insertion with the same palp and chewing-like movements (1–8 successive insertions; mean 3.7)—the male walked around the female through the silk threads up to the other side (mean delay: 1 min)—insertion with the other palp—disinsertion, chewing-like movements, reinsertion and so on. The male carried out approximately 140 palpal insertions and changed sides 38 times during a 144 min period. Mean insertion duration and mean period spent in one side were estimated to be 40 s and 3.3 min, respectively. Three times the male appeared disoriented when walking around the female (total delay: 18 min). The male also adopted atypical positions (ventral - ventral, ventral - dorsal, face to face).

After copulation the male immediately made a sperm induction. The palps alternated four times in contacting the sperm, during 10.5 min. At 216.7 min the female placed herself in contact with the male, and both remained immobile until the following day. During days 2 and 4 the female ate the male, and after some time after she had offspring.

Females of pairs 2 and 3 molted during the night (at days 1 and 9, respectively) and consequently copulations were not seen. Thereafter, both males and females of each pair remained in contact 4 and 3 days, respectively. Female attacks were later observed in both pairs. Afterwards, the male of pair 2 was taken out and placed with the female captured beside pair 2. This female had molted five days before (9 days after capture). Copulation occurred on the first day; although observation was incomplete, it proved to be similar to the copulation of pair 1. The male and female remained in contact during 4 days following copulation. All the observed females produced young.

Cohabitation in *Ixeuticus martius* would be determined both by the male's capacity to recognize subadult females and by tolerance toward

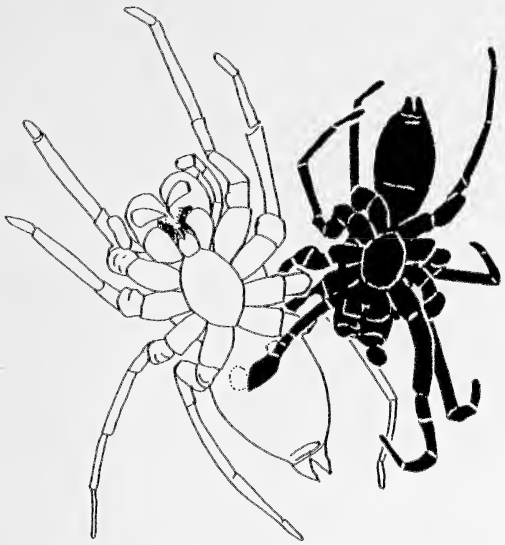

Figure 1.—Copulatory position of *Ixeuticus martius*, pair 1, ventral view. The male (shaded spider) inserts its left palp on the epigynum of the female (white spider). The web's silk threads are omitted.

males shown by females. Resident males probably keep other males away from females (female guarding)—based on field observation of the behavior shown by the two males (pair 2), and the presence of a single male in the other webs. The end result of copulation suggests that cohabitation is a mating tactic: the male safeguards his first insemination and prevents the female from copulations with other males. Austad (1984) analyzed mating tactics and sperm priority patterns in spiders. He hypothetized that males inseminating first ("first male sperm priority") should have greater success than subsequent males in spiders with "conduit spermathecae". Supporting this prediction, Jackson (1986) reported 161 spider species showing precopulatory cohabitation, including six Amaurobiidae species (*sensu* Lehtinen 1967). Only seven of these 161 species had "cul de sac spermathecae". On the other hand, postcopulatory cohabitation is rare and it has not been reported previously in Amaurobiidae, in spite of observations of this sort in Dictynidae (Montgomery 1903; Starr 1988). A female that copulated five days after molting suggested that the 2–4 day tolerance period would be more related to copulation than to adult female age.

The copulatory position of *Ixeuticus martius* is similar to that of *Metaltella simoni* (Prandi pers. comm.) but differs from the typical Amaurobiidae position: the male placed ventrally to female, following a face-to-face encounter (Gerhardt 1923, 1924; Gregg 1961; Leech 1972). The copulatory pattern of *I. martius* (both numerous brief insertions and side changes) is also unusual for the Amaurobiidae's pattern (few and prolonged insertions, multiple ejaculations for each insertion). These differences may not be attributed to the immediate postmolting female state because the copulation with a mature female was similar. The Australian amaurobiid spider *Ixeuticus longinuus* makes an intermediate number of palpal insertions with long pauses (Gregg 1961) and would be the most similar to that of *I. martius*. The literature was revised bearing in mind the controversial placement of several species among the families Amaurobiidae, Dictynidae and Desidae (Lehtinen 1967; Forster 1970; Forster & Wilton 1973), and it showed similar position and general copulatory pattern in Dictynidae (Jackson 1979; Starr 1988) as compared to Amaurobiidae. Singularities showed by *I. martius* could be useful in future (and urgently needed) studies on the systematics of these families.

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Figures 27–34.—Right chelicerae of species of *A-us* from Timbuktu: 27, 29, 31, 33. dorsal views; 28, 30, 32, 34, prolateral views of moveable finger; 27, 28. *A-us x-us* holotype male; 33,34. *A-us y-us* male. Scale 1.0 mm.

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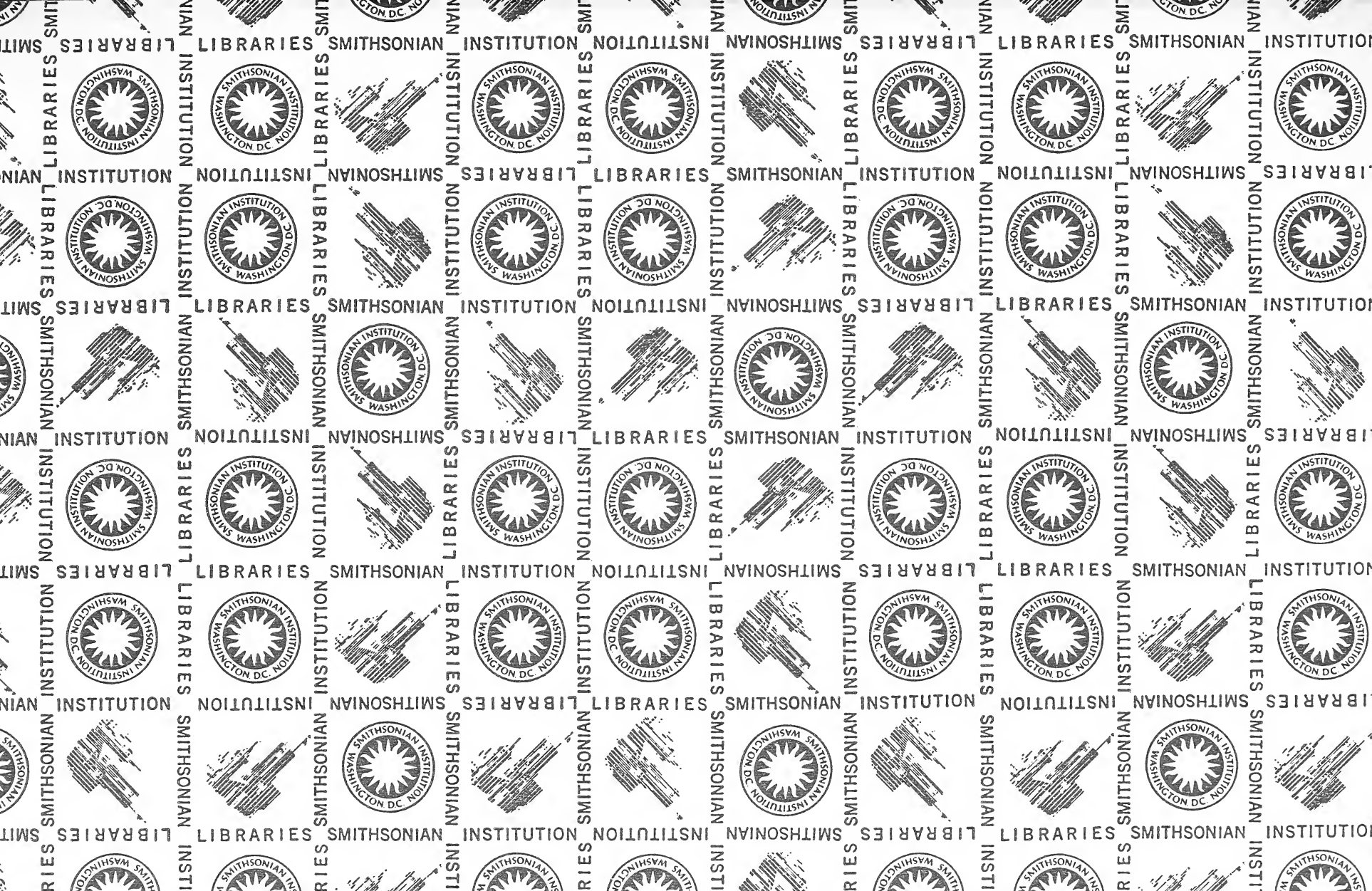
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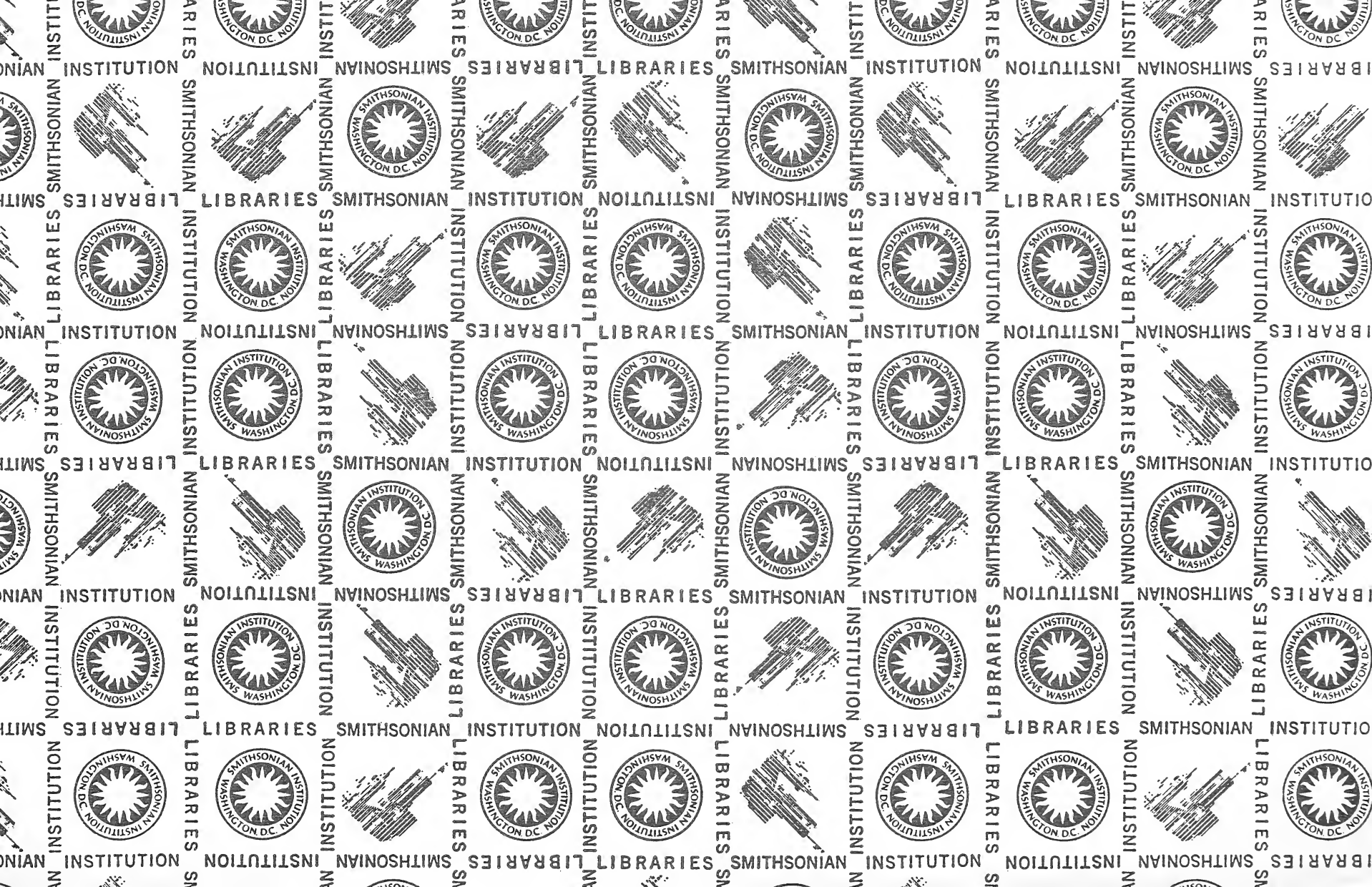
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